BULLETIN

OF THE

FLORIDA STATE MUSEUM

BIOLOGICAL SCIENCES

Volume 4 Number 10

THE ATLANTIC LOGGERHEAD SEA TURTLE, CARETTA CARETTA CARETTA (L.), IN AMERICA

I. NESTING AND MIGRATION OF THE ATLANTIC LOGGERHEAD TURTLE

David K. Caldwell, Archie Carr, and Larry H. Ogren

II. MULTIPLE AND GROUP NESTING BY THE ATLANTIC LOGGERHEAD TURTLE

David K. Caldwell, Frederick H. Berry, Archie Carr, and Robert A. Ragotzkie

III. THE LOGGERHEAD TURTLES OF CAPE ROMAIN, SOUTH CAROLINA

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UNIVERSITY OF FLORIDA
Gainesville
1959

The numbers of THE BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES, will be published at irregular intervals. Volumes will contain about 300 pages and will not necessarily be completed in any one calendar year.

OLIVER L. AUSTIN, JR., *Editor*

The publication of this number of THE BULLETIN has been made possible by a grant from the Graduate School, University of Florida.

All communications concerning purchase or exchange of the publication should be addressed to the Curator of Biological Sciences, Florida State Museum, Seagle Building, Gainesville, Florida. Manuscripts should be sent to the Editor of the BULLETIN, Flint Hall, University of Florida, Gainesville, Florida.

Published 3 June 1959 Price for this issue $.70

THE ATLANTIC LOGGERHEAD SEA TURTLE, *CARETTA CARETTA CARETTA* (L.), IN AMERICA

DAVID K. CALDWELL, ARCHIE CARR, and others

COORDINATORS' PREFACE

When the series of studies now being carried on under National Science Foundation sponsorship (NSF project G-1684 and G-5479, principal investigator Archie Carr) was planned it was proposed that the Atlantic green turtle, *Chelonia mydas mydas* (Linnaeus), be made the central subject of the research. The herbivorousness of green turtles was visualized as imposing on them a distinctive way of life, involving long periodic journeys between feeding and breeding grounds. This, in turn, was seen as a unique attribute, setting *Chelonia* off from other sea turtles—making it easy to study because it gathers to breed in rookeries, and especially interesting because the journeys to and from the rookeries posed special problems of orientation and suggested that *Chelonia* must have an extraordinary capacity to navigate. While all this still seems true, it is now clear that differences among sea turtles with respect to reproductive travel are less than was supposed.

Data from a tagging program at Tortuguero, Costa Rica, have been strengthening the credibility of fishermen's tales of navigatory feats by green turtles. These stories constituted the original assumption to be tested by the Tortuguero studies, and while final proof of their authenticity will be difficult to get, there remains no real doubt of their essential truth. While the case for the navigatory prowess of *Chelonia* has been growing, information from various other sources has suggested that *all* sea turtles migrate.

The following suite of papers supports our belief that the life cycle of the carnivorous Atlantic loggerhead, *Caretta caretta caretta* (Linnaeus), may in most ways be much more similar to that of the green turtle than we imagined. Like the green turtle, the loggerhead travels far, it travels in groups, it emerges more than once to complete a season's laying, it tends to return to the same place for successive layings and is able to locate these sites with some precision, and its breeding range includes places where aggregated nesting occurs as well as sites of separate emergence by lone individuals. Details of nesting and development of the young and their early behavior also are surprisingly similar for all the sea turtles.

To most people, including most zoologists, the loggerhead is an animal to be seen on the sea beach as a nesting female or an emerging hatchling, or at shipside or dockside as a big head stuck up out of the water to breathe. We really know almost nothing about what goes on between these few points of our contact with the animal. Though the information that can be added is fragmentary, it fits in with the fishermen's stories and our growing belief in the essential consonance of the life cycles of all the sea turtles.

The three papers on loggerheads included in this series were prepared independently. They are closely related, even overlapping in some aspects, and it was felt that workers in herpetology and marine ecology would find it convenient to have them available under one cover. We, and the various other authors, are indebted to our respective organizations for permitting, and to the editorial staff of the Bulletin for countenancing this unorthodox style of presentation.

David K. Caldwell, United States
Fish and Wildlife Service,
and
Archie Carr, University of Florida,
Coordinators.
March, 1959

I. NESTING AND MIGRATION OF THE ATLANTIC LOGGERHEAD TURTLE [1]

David K. Caldwell,[2] Archie Carr,[3] and Larry H. Ogren[4]

Synopsis: Tagging evidence shows that female Atlantic loggerhead sea turtles may travel as much as 1000 shoreline miles away from the nesting beach in 10 months.

The nesting procedure of the Atlantic loggerhead is described and illustrated. The loggerhead sometimes nests singly, but more often in aggregations on restricted stretches of beach. Loggerheads mate in the water just off the nesting beach, though whether before or after nesting, or both, is still unknown. No correlation exists between the size of the turtle and the time of laying or the number of eggs laid.

The principal nesting range of the subspecies is the mainland coast of North America from about Cape Lookout, North Carolina, to Mexico; emergences have been recorded occasionally on certain northern Caribbean islands and as far south as Costa Rica. The Atlantic and Pacific subspecies of the loggerhead cannot be separated by their marginal laminae.

Despite the large size of the Atlantic loggerhead turtle, *Caretta caretta caretta* (Linnaeus), and its common occurrence along heavily populated shores, its movements and certain details of its nesting habits are still poorly known. This is an account of recent observations on the species' nesting and of results of tagging operations on the coasts of Georgia and Florida.

Migration

Long Range Travel

It has long been suspected that the stray loggerheads found occasionally in European waters were individuals from American waters, where the nearest upstream nesting grounds lie (in relation to the Gulf Stream). Although it may never be possible to prove the Amer-

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[1] Field work supported in part by National Science Foundation Grants G-1684 and G-5479 (University of Florida, Principal Investigator Archie Carr). Contribution number 42 from the United States Fish and Wildlife Service Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia.

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ican origin of the European loggerheads, and while it may eventually be shown that they derive from downstream rookeries, on the Mediterranean coasts for example, we now at least have a tag return which proves an impressive distance traveled between known points during a known period of time.

The turtle recovered was a female with a carapace length (measured as described by Carr and Caldwell, 1956: 4) of 35 inches, tagged by Caldwell and Thomas R. Hellier, Jr. while nesting at Hutchinson's Island, opposite Jensen Beach, Martin County, Florida, on 27 May 1957. It was recaptured by a shrimp trawler off the mouth of the Mississippi river, probably near Pass-a-Loutre, about 24 or 25 March 1958. It was thus at liberty for about 302 days and was retaken about 1000 shoreline miles from the place of tagging. To reach the point of recapture by the shortest route without crossing the open Gulf, this turtle had to travel southward around the tip of Florida and then northward and westward into the north-central Gulf of Mexico. The length of time between tagging and recapture suggests the animal may have taken a more circuitous inshore route. Although the trip might seem to imply continuous travel against the Gulf Stream, an examination of major seasonal current systems in the Gulf of Mexico (as given by Leipper, 1954: 121-122) shows that the turtle might actually have been helped by currents. Caldwell, Berry, Carr, and Ragotzkie (1959 herein) show that loggerheads nest more than once a season. Although by no means proved, it also seems likely that they remain in the general vicinity of the rookery area throughout the nesting season, or until late summer. If this turtle left the Jensen Beach area in late August, it could have passed around the southern tip of Florida free of opposition by the Gulf Stream simply by staying close inshore until it reached Florida Bay. From the southeastern Gulf of Mexico the currents flowing generally northward and westward along the eastern Gulf coast in the late winter and early spring could have helped it reach the Mississippi by March. This is one of the longest journeys ever proved for any reptile, being rivalled only by trips made by female green turtles tagged in Costa Rica (Carr and Ogren, Ms.).

The only other tagged loggerhead recovered an appreciable distance from where it was marked made a much shorter journey in much less time. Caldwell, Carr, and Hellier (1956b) reported an individual tagged when nesting at Fort Pierce, (Hutchinson's Island, Florida), and recaptured 3 weeks later by a shrimp trawler off Daytona Beach, Florida, some 130 shoreline miles northward. The recovery indicates that mature loggerheads may travel considerable distances in a fairly short period of time. This turtle, like the other, could have been helped by ocean currents, in this case the northward-flowing Gulf Stream.

Movements of the Hatchling

One of the major problems in the study of sea-turtle life histories is the question of where the post-hatchlings spend the first months after they leave the nest. It has been pointed out (Deraniyagala, 1939; Carr, 1952) that small specimens of the Atlantic ridley sea turtle, *Lepidochelys kempi* (Garman), occasionally reach points far distant (England, for example) from their probable natal beaches. Such occurrences suggest a passive migration in the form of a post-hatchling drifting in the major ocean currents, the Gulf Stream in particular. The ridley is the only species in which this conjecture has been supported by concrete evidence, and even this is meager.

We know of no previous records of sea turtle hatchlings taken away from a nesting beach or at sea. Two recent captures are thus of interest. William W. Anderson took a young loggerhead in a dipnet at the surface in 200-fathom water at 25° 10′ N., 80° 02′ W., about 15 miles southeast of Key Largo, Florida, 26 July 1957. This animal, now in the collection of the Bureau of Commercial Fisheries Biological Laboratory at Brunswick, Georgia, still has its egg tooth and umbilical scar and measures 64 mm. in carapace length. Two other hatchlings, one badly macerated, the other in fair condition, were taken from the belly of a 7-foot female white-tipped sharp (*Carcharhinus longimanus*) caught at 30° 50′ N., 78° 45′ W., 135 miles due east of Cumberland Island, Georgia, 22 August 1957. These specimens, now in the University of Florida Collections, show juvenile characters and measure 47.5 mm. in carapace length. They were sent us by Dr. Richard Backus of the Woods Hole Oceanographic Institution, who has been consistently generous with sea turtle data gathered incidental to his oceanographic studies.

Comparison with captive loggerheads of known age (cf. Caldwell, Carr, and Hellier, 1956b: 297) suggests the first specimen was about 11 weeks old, the second two about 12 to 13 days old when eaten. Whether these turtles were lost waifs drifting to oblivion in the open sea, or whether they occur in these localities regularly after leaving the nesting beaches is still uncertain. If they occur in these waters regularly, it is strange that the biologists who have spent hundreds of hours observing and dipnetting there have reported no others.

Mating and the Nesting Process

Colonial Nesting

Although the loggerhead nests on the beaches of all the coastal South Atlantic and Gulf states roughly from Cape Lookout, North Carolina, to Texas, it apparently concentrates its nesting activity in restricted areas which may conveniently be termed "rookeries." Similar rookeries are known for other species of sea turtles, particularly the green turtle. We have found three such nesting concentrations of loggerheads on the Atlantic coast of the United States; one is Hutchinson's Island, Florida; another is Jekyll Island and the adjacent Little Cumberland Island near Brunswick, Georgia; the third is Cape Romain, South Carolina, fortunately located within a United States Fish and Wildlife Service wildlife refuge. Aerial reconnaissance of the coast of Florida north of Matanzas Inlet, of the entire coast of Georgia and of most of that of South Carolina, has shown the apparent concentration of nesting activity on Jekyll and Little Cumberland Islands and at Cape Romain to be real. While a few nests were observed scattered along the entire stretch of coast, each flight showed the places mentioned to be far more heavily used than any other area. Surveys of the south Florida coast indicate that Hutchinson's Island is similarly important as a rookery.

In addition to the concentration of tracks seen from blimps on Jekyll and Little Cumberland Islands, evidence that these islands near Brunswick are used as a rookery has been supplied by William W. Anderson. While conducting shrimp studies for the Fish and Wildlife Service with the Brunswick shrimp fishery off the Georgia islands, particularly from 1930 to 1938, he found loggerheads quite rare in the area each year during the fall, winter, and early spring. In late spring as the summer nesting season approached, the turtles appeared in large numbers in these particular waters, and were seen nowhere else in abundance, neither off neighboring islands nor in the sounds and passes. The turtles off Brunswick were at times plentiful enough to be a nuisance to the shrimp fishermen whose trawls they damaged. As shrimping continued after the turtle nesting season, it provided a good sampling opportunity, which indicated a real influx of mature-sized loggerheads from outside the rookery area during the nesting season. Brunswick shrimp fishermen working today say that although the total loggerhead population has been reduced, this same seasonality in abundance occurs.

Mating

In both the Atlantic and Pacific green turtles mating occurs mainly off the nesting beach (Harrisson, 1954; Carr and Giovannoli, 1957: 30.). William W. Anderson's observations suggest that similar behavior is characteristic of loggerheads. He had excellent opportunities between 1930 and 1938 to observe the turtles clearly from his slow-moving trawler, and states that he often saw loggerheads mating in the water just off the Georgia beaches, particularly near the passes between the sea islands where the beaches are located. Not being aware at the time of the scarcity of such data, Anderson kept no records of dates, but he clearly recalls that this mating behavior took place each year he worked in the area, and always during the nesting season of the loggerhead. His observations agree with those of others that mating loggerheads tend to ignore a nearby boat. He never saw mating turtles in threes—a female with two attending males—as has been reported for the green turtle by Carr (1956) and by Carr and Giovannoli (1957: 31); although elsewhere we have been told of observations of such trios of loggerheads (see also Caldwell, 1959, herein).

Anderson noted that the influx of turtles to the waters off the nesting beaches began as much as a month before actual nesting. This fact may bear on the problem of whether mating occurs just before laying or afterwards, a detail not yet determined for any species of American sea turtle (Carr and Giovannoli, 1957: 31; Carr and Ogren, Ms).

Nest Building and Oviposition

Although the nesting of the Atlantic loggerhead frequently has been described in popular articles, the only accounts in zoological literature that recount the process in detail are the composite descriptions of Mast (1911) and Carr (1952: 390). After observing nesting loggerheads for several seasons we find that these accounts require modification. Accordingly we present the following description of the nesting of the Atlantic loggerhead and the accompanying series of photographs showing some of the more important details. Both the notes and pictures are composites, because it is difficult to find turtles just emerging from the sea and to follow and photograph the entire procedure of a single individual. However, the behavior was so similar in all localities and at all times of the nesting season that the account given here is believed to be representative of the Atlantic loggerhead on the coasts of Florida and Georgia.

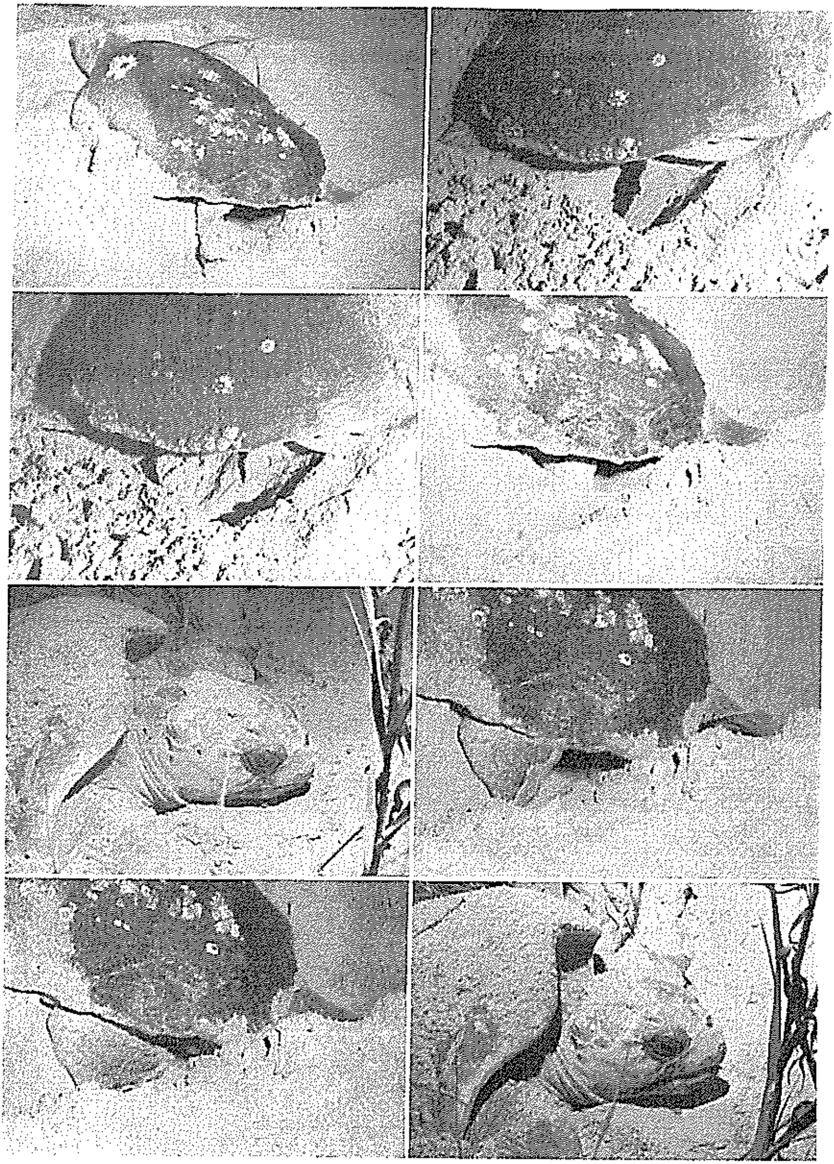

Figure 1.—Nesting Atlantic loggerhead, showing large excavation made preliminary to actual digging of nest (see text).

Figure 2.—Flipper inserted into growing nest cavity.

Figure 3.—Flipper lifting sand out of nest cavity.

Figure 4.—Left flipper digging, right flipper flat on sand.

Figure 5.—Head down and neck arched prior to laying. Note open eye and tears.

Figure 6.—Hind flippers raised before group of eggs is extruded.

Figure 7.—Hind flippers lie flat on surface of sand during intervals between extrusions of eggs.

Figure 8.—Head raised between extrusions of eggs. Note tears and open eye.

On first leaving the water, and even until she has started to dig, the turtle is easily disturbed. She reacts strongly to a light thrown directly upon her. Contrary to Carr's account (1952: 390), after the site for the evening's activity is selected all turtles observed dug a preliminary excavation of varying extent. The female uses all four flippers in this process until she has lowered herself several inches below the surface of the sand (Figure 1). Digging of the actual nest follows almost immediately, for which only the hind flippers working alternately are used. With its outer edge downward, one flipper is inserted into the sand or into the growing hole (Figure 2). It is then cupped, and the outer edge is rotated inwardly. A small amount of sand is now scooped up (Figure 3), lifted to the top of the hole, and deftly laid to one side. Meanwhile the opposing flipper remains flat, "palm" down on the sand near the edge of the hole (Figure 4). The turtle now shifts her body so this other flipper comes into position over the hole. Just before she inserts it into the hole to dig, she flicks it out laterally and upward to brush the loose sand, deposited when this flipper last excavated, away from the edge of the hole. This technique differs only in minor points from that described for the green turtle by Carr and Giovannoli (1957: 25).

The digging process is then repeated as the turtle shifts to bring the first flipper into play again. Almost as soon as the nest is finished the flippers are laid straight back or pointed slightly outward, "palms" down (Figure 7), and the cloacal "ovipositer" is inserted. During the digging process the head has been held flat on the sand and the eyes kept open, although blinking occasionally. The eyes secrete copiously (Figures 5 and 8) during the digging and laying. Just before each group of eggs falls (in groups of one, two, or three) the neck is arched with the head still down (Figure 5), and the hind flippers are raised slightly (Figure 6). As each group of eggs falls, the neck is lowered to the position held during digging and the flippers come down and lie flat again between extrusions (Figure 7). During this interval, the head may be raised slightly (Figure 8) and the turtle may snort or sigh by expelling air from her nostrils or mouth.

Carr and Giovannoli (1957: 25) stated that the loggerhead will press its vertically oriented back flippers against the upper part of the wall of the nest cavity "as if to keep sand from falling in," and Carr (1952: 11) illustrates the maneuver in *Lepidochelys*. Despite numerous attempts, we never succeeded in bringing about this behavior in a laying Atlantic loggerhead. Several times we dug part of the wall of the nest away to reveal the eggs for photography, and never did the

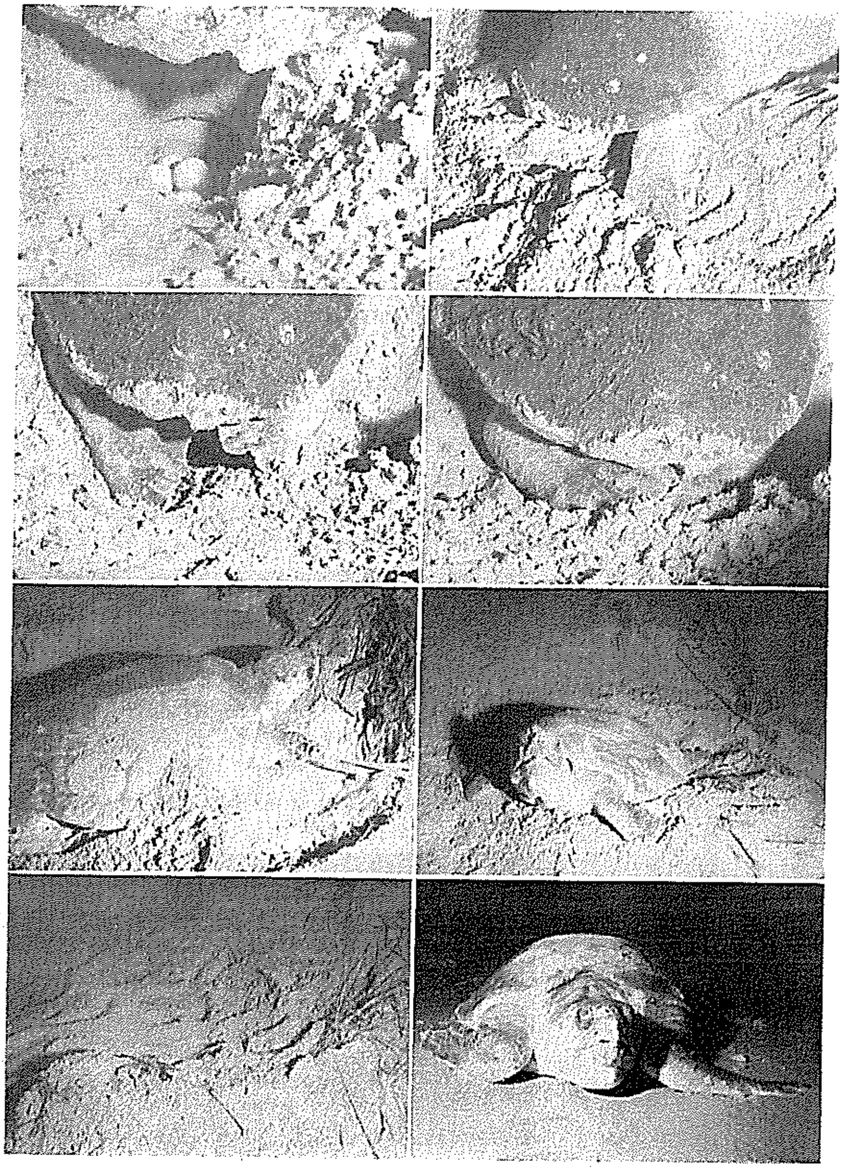

Figure 9.—Nearly cylindrical nest cavity almost filled with eggs.
Figure 10.—Rear flipper dragging sand to fill nest and cover eggs.
Figure 11.—Hind flippers packing sand in filled nest.
Figure 12.—Hind flippers packing sand in filled nest.
Figure 13.—All flippers sweeping sand to conceal the site.
Figure 14.—Turtle about to leave the nest. Note lifted head, open eye, and prominent hyoid apparatus.
Figure 15.—Nest site after departure of turtle. Trail leads off to left.
Figure 16.—Turtle crawling to the surf after nesting. Note position of head.

turtle attempt to shore up the crumbling nest. Once when we moved the posterior end of the turtle away from the nest opening she continued to lay on the surface of the sand beside it. When replaced over the hole, she continued to lay as if nothing had happened.

When the nest is filled with eggs (Figure 9), covering begins almost immediately. Sand is drawn in by the hind flippers, usually working alternately, sometimes together. The outer edge of the flipper is used, the limb reaching well forward and out from the body to drag sand back to the hole (Figure 10). As filling proceeds, the front flippers join in sweeping sand backward to replenish that pushed into the nest cavity by the hind legs and, like the hind flippers, the front ones are used either alternately or together. When the hole is full of loose sand, the hind flippers press it down firmly (Figures 11 and 12). During the filling and packing process the head and fore part of the body are sometimes raised as if to shift weight to the hind flippers and help them exert more force. Perhaps this shifting and raising of the body to increase pressure at the hind flippers accounts for the impression that the site is "pounded." Although it was expressly watched for, no turtle was seen to pack or pound the nest with her plastron, as reported by Carr (1952: 391). As the filling reaches completion, the front flippers aided somewhat by the hind ones begin to fling sand backward. This increased exertion pivots the turtle on the pedestal of sand her digging leaves under her plastron.

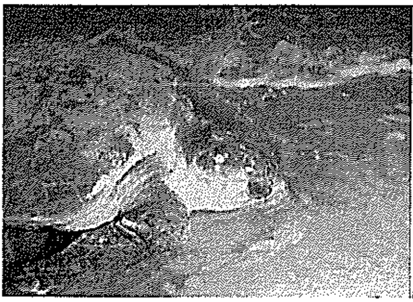

Figure 17.—Arrival at water, snout lowered into surf.
Figure 18.—Head raised before turtle proceeds through surf.

After completing the nest the turtle rests for a short period, and she also rests between the several subsequent outbursts of sand-flinging before moving away from the site. The flinging of sand—presumably aimed at concealing the site, and certainly effective—often enlarges the preliminary excavation (Figure 13). Just as the turtle moves away from the site she raises her head high with the eyes still open, as they have been throughout the nesting process (Figure 14), and the hyoid apparatus becomes quite prominent as it moves in and out. When she leaves the nest, the site (Figure 15) is so camouflaged that the eggs are hard to find without the aid of a probing rod.

The return trip to the surf is usually made quickly and purposefully. Although the head is slightly raised while the turtle drags herself along (Figure 16), on reaching the water she drops her head into it (Figure 17). After a moment she raises it again (Figure 18) before moving rapidly out of sight into the sea.

Agent Robert Kilby of the Georgia Game and Fish Commission has told us of turtles completing the digging activity, laying a few eggs, beginning to cover these, and then laying the rest of the complement before finally covering the nest.

One collaborator let a turtle complete her nest, and when he turned her to be tagged she layed another mature egg. We allowed one turtle to finish her nest and then killed her to examine her for internal eggs. Though she had laid 90 eggs in a normal fashion and covered her nest, she still retained two mature eggs in the lower oviduct.

While the size of each egg in a clutch remains fairly constant, unlike those of the leatherback, *Dermochelys coriacea coriacea* (Linnaeus), (see Caldwell, Carr and Hellier, 1956a: 282; Caldwell, 1959; Carr and Ogren, in press) we twice found a single tiny egg in a normal clutch at the Jekyll Island rookery. These small eggs, somewhat oblong and measuring about 20 mm. in their greatest dimension, were fully shelled but contained no yolk and only a small amount of albumen. It was not ascertained when they were deposited.

Time of Emergence

Nesting loggerheads usually come out of the sea shortly after dark, and most of their nesting activities take place during the first 4 or 5 hours after dusk (see Caldwell, 1959, herein). As no case of a loggerhead nesting after daylight has been reported in the literature, the following observations are of interest.

On 13 July 1958 Caldwell, in company with Frederick H. Berry and Robert A. Ragotzkie, made a low-altitude aerial survey of the sea beaches from Cape Romain, South Carolina, to Brunswick, Georgia. At 0905 hours they observed a large loggerhead just returning to the water after apparently having nested on a beach just north of the inlet to Charleston Harbor, S. C. Official sunrise was 0500 hours and, as the day was clear, it was full daylight by 0545. The tide had just turned to flood and, as the tracks leading out of the water extended nearly to the water's edge, the turtle could not have been on the beach more than the normal hour or so. From the air it appeared that this turtle had started and completed a normal nesting during full daylight.

During mid-July 1954 Agent Robert S. Pfister of the Florida State Board of Conservation made a similar observation on Hutchinson's Island about 1 mile south of the Fort Pierce Inlet where he had noted little preivous nesting. A rather small turtle appeared on the beach before sunrise when the dawn was just light enough so that "one would not need lights to drive a car on the highway." The turtle made a leisurely but direct trip to a spot above the high tide mark, dug its nest, laid, covered the eggs, and returned to the water. By then the sun had been above the horizon for a full hour.

A third instance, by coincidence also on 13 July 1958, was reported by Agent Kilby, who saw a turtle on Jekyll Island covering her eggs well after daylight. He believed that she must have left the water at about 0530 to 0600 hours, well after daylight. Kilby found another loggerhead after daylight on the south end of Jekyll Island which he thinks was lost on the broad sand flat, for her back trail was unusually long and meandering.

Agents Pfister and Kilby guard two of the three greatest loggerhead nesting grounds on the entire Atlantic coast of North America. They patrol the beaches in their charge with motor vehicles nearly every night throughout the turtle nesting season, from just after dark to past dawn. They undoubtedly see most of the turtles that emerge on their beaches, possibly more than are seen by any other men alive.

Size of Nesting Females

Carapace lengths to the nearest one-fourth inch were recorded for 110 turtles nesting on Jekyll Island from 29 May through 31 July 1958. The mean length was 37¾ inches, with a range of 31¼ to 45¼ inches. An analysis showed no correlation between the size of the turtles (either mean or range) and the dates they nested.

Size of Turtle in Relation to Number of Eggs Laid

The number of eggs in 25 clutches was compared with the size of the turtles laying them. Analysis of these variables showed no correlation.

Nesting Range

Each year since Carr's first visit to Tortuguero, Costa Rica, in 1953 the local turtle-turners there have reported the emergence of a loggerhead or two among the green turtles, Atlantic hawksbills (*Eretomochelys imbricata imbricata* (Linnaeus)), and Atlantic leatherbacks (*Dermochelys coriacea coriacea* (Linnaeus)). Though hundreds of turtles were examined there during the tagging program (Carr and Giovannoli, 1957; Carr and Ogren, in press; Carr and Ogren Ms.) no loggerhead was found until the summer of 1957, when early in the evening of 29 July a small (carapace length 34 inches) female came out on the beach and was turned by Durham Rankin, a creole in the employ of the project (Figure 19). The southernmost previous recorded emergence for the loggerhead was from the north coast of Cuba (Caldwell, Carr, and Hellier, 1956b: 296), though Lewis (1940: 62) noted that the species is reported to nest on the Cayman Islands.

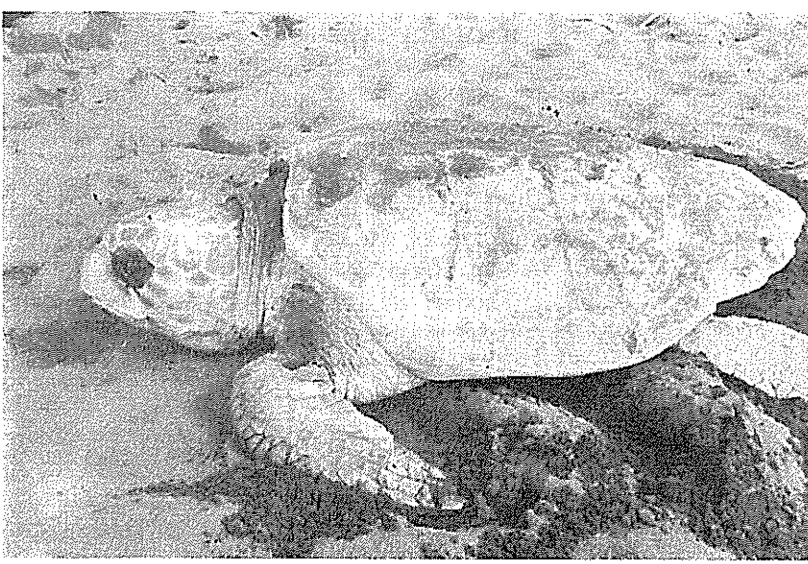

Figure 19.—Female loggerhead photographed on the beach at Tortuguero, Costa Rica; the first emergence recorded for the species in American waters south of Cuba.

The case presents an extreme example of the tendency, observable in other species of marine turtles and mentioned earlier in this paper as characteristic of loggerheads of the Atlantic coast, to nest either in aggregations or as isolated individuals. Breeding aggregations of animals usually develop integrating bonds that place the aberrant individual with an urge toward solitary breeding at a selective disadvantage. The chances for consummation of any reproductive venture apart from the group effort, especially when a long migration to the nesting grounds is involved, would appear slight. With the sea turtles we can at present only point out the phenomenon and hope that with better understanding of the organization of the breeding group an explanation will eventually emerge.

Variation in Marginal Laminae

One character used to distinguish between the Atlantic and Pacific subspecies of the loggerhead has been the number of marginal laminae; the Atlantic form is supposed usually to have 12 on each side and the Pacific race 13 (see, for example, Carr, 1952: 382). Counts of the marginal laminae in two small groups of hatchlings, each group from a single clutch of eggs and both from Jekyll Island, show this character to be invalid. In one group 8 specimens had a 13-13 count, 4 a 12-12. The other group had 5 with a 13-13 count, 6 with 12-12, and one with 13 on the left and 12 on the right.

Acknowledgments

We wish to thank the many people who furthered our studies with information, physical aid, and encouragement. Some of these are: Frederick H. Berry, Harvey R. Bullis, Jr., Rolland C. Byrd, Mr. and Mrs. Henri Casanova, Hugh M. Fields, David Gould, Evelyn Hellier, Thomas R. Hellier, Jr., James R. Pearce, Teodoro Quiros C., and Robert A. Ragotzkie.

We are grateful for the cooperation afforded the project in Georgia by the United States Navy (Naval Air Station, Glynco) which granted permission to make reconnaissance flights in their airships. David Gould, Director of Coastal Fisheries for the Georgia Game and Fish Commission, kindly allowed Caldwell to participate in patrol flights by the Commission airplane. The pilot, Clifford G. King, was most gracious in facilitating observations during the flights.

We are especially indebted to Agents Robert Kilby and Robert S. Pfister, respectively of the Georgia Game and Fish Commission and the Florida State Board of Conservation, for their untiring cooperation in the field. Officials of both these agencies were most helpful in granting us collecting and study permits. William W. Anderson generously furnished us with important unpublished notes on Georgia sea turtles; and to him, to Frederick H. Berry, and to Jack W. Gehringer we are indebted for critical reading of the manuscript.

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II. MULTIPLE AND GROUP NESTING BY THE ATLANTIC LOGGERHEAD TURTLE [5]

DAVID K. CALDWELL, FREDERICK H. BERRY,[6] ARCHIE CARR, and ROBERT A. RAGOTZKIE[7]

SYNOPSIS: Tagging results and studies of unlaid eggs in dissected females demonstrate that individuals of the Atlantic loggerhead sea turtle nest several times on the same stretch of beach in a summer, but it is not yet known whether each individual lays every year. Individual turtles can locate these places with some precision. Tagging results show groups of turtles nest together several times, and it is believed they stay together during the periods between the nesting emergences.

Although fishermen, turtle poachers, and conservation officers commonly believe that the Atlantic loggerhead sea turtle, *Caretta caretta caretta* (Linnaeus), lays more than once during a season and that groups of turtles remain together during the season to nest together, no detailed observations on these points appear to have been made by biologists. Recent evidence of tagging studies proves multiple emergence and suggests group adherence of individuals. Further evidence that the eggs of a season are laid in two or more batches has been the finding of unlaid eggs in discrete size groups in female turtles dissected during the nesting season. Counts and measurements of such eggs are included in the present paper.

GROUP NESTING EMERGENCE

In examining their tagging data on the green turtle, *Chelonia mydas mydas* (Linnaeus), for possible evidence of group travel, Carr and Giovannoli (1957: 9) found cases in which individuals that emerged together tended to return to renest together later the same season. We have clumped tag returns that suggest similar group movements in nesting *Caretta*.

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[5] Field work supported in part by National Science Foundation Grants G-1684 and G-5479 (University of Florida, Principal Investigator Archie Carr) and by the Georgia Game and Fish Commission. Contribution number 43 from the United States Fish and Wildlife Service Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia.

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Our first evidence for grouped emergence resulted from limited tagging studies conducted in 1957 at Hutchinson's Island near Fort Pierce, Florida. While not so impressive as the results obtained at Jekyll Island near Brunswick, Georgia, in 1958, to be described below, they nevertheless suggest that group movements may be the rule in loggerheads.

On 27 May 1957 seven nesting loggerheads were tagged on Hutchinson's Island with monel cow-ear tags (Carr and Caldwell, 1956:3) fixed to the front flipper, including one numbered 78. On 28 May 1957, 11 turtles were tagged, including one numbered 23. Number 23 was released within 2 miles of the release point for number 78.

At 0115 hours on 30 June 1957, 34 days after the first tagging date, Agent Robert S. Pfister of the Florida State Board of Conservation found number 23 nesting "7 miles south of the Ft. Pierce Inlet," at approximately the same place where she had been tagged. At 0120 hours only a short distance away, a few hundred yards at most, he found number 78 nesting. In spite of the small size of the sample, the fact that this double return involved two out of a group of only 18 turtles tagged makes it highly improbable that the dual recovery was due to chance. This double return and a long-range recovery in the northern Gulf of Mexico from the 27 May tagging (Caldwell, Carr, and Ogren, 1959, herein) are the only reports to date from 72 turtles tagged on Hutchinson's Island during the 1957 season. This lends significance to the dual recovery and enhances its value as evidence of concurrent movements.

TABLE 1

NUMBERS OF TURTLES TAGGED AT JEKYLL ISLAND, GEORGIA, IN 1958 WITH MONEL COW-EAR TAGS, AS DESCRIBED BY CARR AND CALDWELL (1956).

early June (date uncertain)	5	9–11 July	4	22 July	1
6 June	6	11 July	5	23 July	1
10 June	4	15 July	6	24 July	2
13 June	7	16 July	7	25 July	3
9 July	4	17 July	6	29 July	1
10 July	1	18 July	6	31 July	3
				Total	72

The results of the 1958 tagging studies on Jekyll Island clearly show this phenomenon of group nesting emergence by loggerheads (table 2). Eight turtles, numbers 125, G43, G47, G103, G105, G107, G108, and G111, show such close agreement in their dates of first and later emergences that they may be considered as one group. Though our records are indefinite on the point, it is presumed that all laid on the night of tagging or very shortly thereafter. This presumption is based on findings (presented below) that show a turtle emerging and failing to nest one night will return the same or suc-

TABLE 2

RETURNS OF LOGGERHEAD SEA TURTLES TAGGED AT JEKYLL ISLAND, GEORGIA, IN 1958. (ld) DENOTES TURTLE LAID; (dnl) DENOTES TURTLE DID NOT LAY, (nd) DENOTES NO DATA ON NESTING ACTIVITY.

Tag Number[8]	Date Tagged	First Return	Second Return	Third Return
110	June 6 (ld)	July 10 (nd)		
111	June 10 (dnl)	June 16 (ld)	July 5[9]	
114	June 10 (ld)	July 23 (ld)	July 29 (dnl)	
117	June (?) (nd)	July 18 (nd)		
118	June 13 (dnl)	June 28 (ld)		
120	June (?) (nd)	July 11 (nd)		
121	June (?) (nd)	July 10 (nd)		
123	June 13 (dnl)	July 29 (ld)		
125	June 13 (dnl)	July 16 (ld)	August 1 (ld)	
136	early June (nd)	June 28 (ld)	July 11 (ld)	
144	June (?) (nd)	July 26 (ld)		
147 / G35 [10]	July 11 (nd)	July 14 (dnl)	July 26 (dnl)	
G30	July 10 (dnl)	July 11 (ld)		
G33	July 11 (dnl)	July 23 (ld)		
G37	July 11 (dnl)	July 15 (nd)		
G43	July 15 (dnl)	July 28 (dnl)	July 29 (dnl)	July 30 (ld)
G47	July 16 (ld)	July 31 (ld)		
G49	July 16 (dnl)	July 17 (ld)		
G102	July 16 (dnl)	July 17 (dnl)	July 18 (nd)	
G103	July 17 (ld)	July 30 (ld)		
G105	July 17 (ld)	July 30 (ld)		
G107	July 17 (ld)	July 31 (ld)		
G108	July 17 (ld)	July 30 (ld)		
G111	July 18 (ld)	July 31 (dnl)	August 1 (ld)	
G115	July 22 (dnl)	July 23 (ld)		
G119	July 25 (ld)	August 7 (ld)		

[8] Tags bearing no letter prefix are marked for return to the University of Florida; those bearing a "G" prefix are marked for return to the Georgia Game and Fish Commission.

[9] Turtle found dead on beach. Oviduct contained shelled eggs.

[10] Turtle re-tagged when original tag pulled out during first recapture.

cessive nights until she nests successfully. Thus these turtles returned together as a group to lay again after approximately 2 weeks.

As turtle 125 presumably laid in mid-June, her record suggests that the group nested at least four times that summer, in mid-June, in late June, in mid-July when most were tagged, and in early August. The probability that the grouping shown by this series occurred by chance alone, especially with so few turtles tagged, is so slight that coincidence need not be considered. Possibly another aggregation on Jekyll is the group made up of numbers 110, 120, 121, 147-G35, and G30, but the data for this and possible other groupings are not conclusive.

Aggregate nesting is also suggested by observations William W. Anderson, United States Fish and Wildlife Service, made during a shrimp study for the Service in Georgia from 1930 to 1938. The investigation involved considerable field work and afforded him the opportunity to observe turtles from a small slow-moving boat. Anderson noticed that during the nesting season turtles were not present at all times in great numbers, but rather that they seemed to arrive in the area in groups. Correlated was the general observation that nesting turtles likewise tended to arrive together on the beach.

Later studies conducted at Jekyll Island by Caldwell and Berry showed a similar phenomenon of groups of turtles on the beach at one time, then periods with only an occasional individual present before another group appeared. Thus, while there was a general congregating of turtles in the area during and just before the nesting season, it appears likely that the turtles did not remain in the immediate vicinity between nesting times, but perhaps moved elsewhere to await their time for returning to renest.

Anderson further noted that at no time during the season were turtles abundant in Georgia waters other than those immediately surrounding the rookeries at Jekyll and Little Cumberland Islands. It seems unlikely that the turtles return to their wintering grounds between nestings and regroup before returning for the next nesting venture. There remains for the loggerhead, as for the green turtle (Carr and Giovannoli, 1957; Carr and Ogren, Ms.), the stubborn problem of where they go in the interim. They may go offshore, but observations do not support this.

Multiple Nesting as Shown by Tagging Results

We referred earlier to a return to the Hutchinson's Island beach by two turtles that had nested there about a month before. In the

Atlantic green turtle the interval between the nesting ventures of a season is 12 to 14 days (Carr and Giovannoli, 1957; Carr and Ogren, Ms.). A similar interval was suggested for the loggerhead by Lewis (1940: 62), which our recoveries at Jekyll Island corroborate. Presumably the recovery of the two turtles at Hutchinson's Island after a month's absence must have been preceded by an unrecorded return 2 weeks earlier.

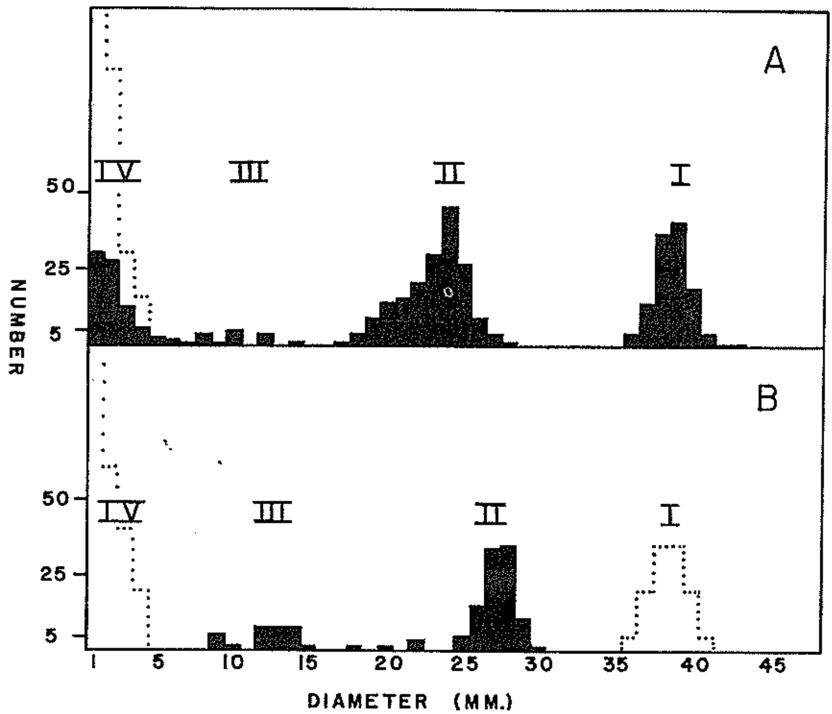

Figure 20.—Diameter-frequencies of freshly laid and ovarian eggs of the Atlantic loggerhead turtle at Jekyll Island, Georgia, in 1957. Solid areas indicate eggs actually measured. Dotted lines indicate estimated numbers of eggs within the indicated ranges of diameters.

From the first week of June through the last week of July 1958, 72 loggerheads were tagged at the Jekyll Island rookery (Table 1). Of these, 26 were recaptured one or more times (Table 2). In addition to these definite records, tourists reported seeing about 10 more tagged turtles on the beach. As no data accompanied these reports they are of no value in piecing out laying schedules.

From our observations, and from those on injury-marked turtles made by others, we believe that a turtle interrupted in her nesting will return either later that night or on successive nights until she has fulfilled her mission. Carr and Giovannoli (1957: 24) reported for green turtles a similar "singlemindedness of the nesting drive," borne out by turtles number 111, G30, G37, G49, G115, and particularly by G43 and G102 (Table 2).

Thus a turtle tagged on a given date but not known to have layed then, can be assumed to have laid within the following few days, and any recovery of a turtle more than a week after the time of tagging theoretically constitutes an example of second nesting (see, for example, turtles number 118, 123, G33, G43, 147-G35 in Table 2).

In every case for which data are adequate, all the instances of multiple nesting on Jekyll Island took place at intervals of 12 to 15 days, with the single exception of number 114. With the 2-week interval between laying emergences shown so convincingly to be standard, it can be presumed that the other tagged animals would have shown comparable intervals had they been caught each time they nested. For example, recoveries of turtles 117 and 144, like the Florida returns noted above, probably represent second nesting emergences after tagging. Turtle 123 may have returned a third time. Turtle 136 definitely laid twice, and the interval between the time of tagging and first corroborated laying is long enough to have permitted a third nesting in the interim, or four nestings for the season. It seems likely that the turtles in the group discussed in the section on Group Emergence laid four times.

Sapelo Island, Georgia, is not considered a "good turtle island," and is not part of the Jekyll rookery. The minimum straight-line distance between the north end of Jekyll and the south end of Sapelo is approximately 19 miles. In 1958 three turtles were tagged on Sapelo Island, one of which (G23) was recaptured there 31 July, two nights after being tagged. She did not nest either time, but the return supports the popular assumption that each turtle nests on a single island, and only on that island, even though concentrated nesting may be going on at a nearby rookery. Another turtle, not tagged but bearing distinctive marks, apparently laid twice on Sapelo, on 18 and 28 June. The interval is short, but the evidence that the same turtle was involved is convincing, and we believe this to be another instance of multiple nesting on an island other than Jekyll. Little Cumberland Island, immediately south of Jekyll, seems from concentrations of tracks seen from the air to be part of the Jekyll rookery, but there is no road to Little Cumberland, and no practical means were available to visit the island at night to look for turtles tagged at Jekyll, or to tag turtles for possible recovery at Jekyll.

Data extracted from a hitherto unpublished report (see Caldwell, 1959, herein) prepared in 1940 by William P. Baldwin, Jr. and John M. Lofton, Jr. show similar results for loggerheads tagged on a rookery at Cape Romain, South Carolina. These workers tagged 18 turtles as they came ashore to nest. Turtle number 4 was tagged but did not lay on 12 June; she was recaptured as she laid on 27 June. It is assumed that she laid soon after the 12th, and the expected 2-week interval between nesting ventures is indicated. Turtle number 13 was tagged but did not lay on 6 July. She was recaptured again not laying on 28 July. The elapsed time clearly indicates attempts at multiple nesting, perhaps three times in the 22 days. Turtle 10 was tagged on 3 July and recaptured on 4 July, nesting neither time. Turtle number 4 returned to a point 1000 feet north of the point of initial emergence; number 13, 950 feet southward; and number 10, 300 feet southward.

Unfortunately some of the people at Jekyll who furnished enthusiastic cooperation in tagging and in recording returns kept only dates of tagging and return and did not record the exact spots involved. It is of particular interest to note that in all cases where exact data were available for tagging and return, the turtle involved returned not only to Jekyll Island, but to the same portion of the island, within ¼ mile of the initial point of tagging on the 10.5-mile beach. None of the many turtles tagged at Jekyll Island was found by observers on Sapelo Island, nor were any of the few turtles tagged at Sapelo recorded as nesting later at Jekyll. The only returns on each island were turtles tagged on that island. Similar homing was noted by Carr and Giovannoli (1957) and by Hendrickson (1958) for the green turtle.

Evidence of Multiple Nesting Based on Unlaid Eggs

Data on egg size groups afford further evidence of multiple nesting and corroborate the tag return data.

Early in the 1957 season an individual designated as turtle A (Figure 20) that emerged on Jekyll Island 23 May was killed for study before being allowed to nest. She contained 120 shelled eggs of mature size (Carr, 1952: 391) she presumably would have laid that night. In addition to the mature eggs, a second group (II) of 182 eggs consisted of large yellow yolks, and a third group (III) consisted of about 25 much smaller yellow yolks. Eggs of size group IV were tiny (4 mm. in diameter or less) white or yellowish spheres and occurred by the thousands. These tiny eggs presumably serve as a reservoir and may be present at all times in mature females. Since the 182 eggs in group II were more than the expected complement for a single laying, it was probable that some of the smaller ones in this group and the larger ones in group IV would have gone to build up the small group III to about the expected 125.

Another individual, designated as turtle B (Figure 20), was killed in mid-season on 1 July, also on Jekyll Island, just after nesting. She had deposited 144 eggs. The groups of smaller eggs in this individual were better defined than those in turtle A. The mature eggs of both turtles (group I in Figure 20) furnish definite evidence for one nesting that season. Considering the two turtles A and B as one composite animal, and postulating that nesting takes place at 2-week intervals, it is reasonable to assume that a laying by this hypothetical single turtle probably occurred between 23 May and 1 July. The group III eggs in turtle A might well have reached mature size in the elapsed month to become group I in turtle B. The fact that the nodes of egg diameters of groups II and III of turtle B are further advanced than corresponding ones in turtle A is further evidence that eggs develop continuously during the season to replace laid clutches of group I eggs.

While these data strongly suggested that multiple nesting occurs in loggerheads, they did not furnish firm grounds for calculating the number of times an individual might nest in a season, nor do the tagging results. One female might not come to the rookery until mid-season or later, and might nest only once or twice. Another might nest very early and thus have time to complete three or more additional layings. Turtle B in Figure 1, for example, might not have nested in early summer, and her egg-groups II and III may forecast two more nestings to take place late in the season. Or if she did nest early, they may represent a third and fourth nesting for the season. Conversely, her group III eggs might have been reabsorbed after the 1957 nesting season. Her group II eggs were large enough to have been destined for laying in the 1957 season, and it does not seem likely that any of her eggs of group IV would have reached maturity by the end of the 1957 season. Possible evidence that reabsorption of eggs occurs is the fact that some of the group III eggs in turtle B were dark purple or black in color as if vascularized for reabsorption.

In another instance turtle number G119 (Table 2) was killed after laying the second time. She had deposited 90 eggs in a normal fashion. Her oviducts contained 57 large yellow eggs approximately 14-30 mm. in greatest diameter which could have forecast a third laying for the season. There is no reason to believe she had not also laid 2 or more weeks before she was tagged. In addition to the large yellow eggs, she also contained about 200 whitish-yellow eggs 5-10 mm. in greatest diameter, and several thousand eggs less than 5 mm. in diameter.

Still another possibility is that the individual might complete a fixed number of nestings at 2-week intervals, no matter when she first arrives at the rookery. Thus, one group of turtles may nest early in the season (say 3 or 4 times during the first 6 weeks), another during the middle 6 weeks, and a third group during the final 6 weeks. As the laying season lasts only about 12 to 15 weeks, the groups of turtles surely overlap in their periods of stay, which could account for the larger number of turtles nesting in mid-season (see Caldwell, 1959, herein). More than three groups of turtles, or one turtle nesting more than three times, which our tagging studies suggest occurs, would further complicate such a nesting regime, but not make it impossible.

Acknowledgments

We are indebted to a number of people who furthered our studies by supplying information, physical aid, and encouragement. Some of these to whom we owe special thanks are: William W. Anderson, Carolyn Berry, Hugh M. Fields, Jack W. Gehringer, Evelyn Hellier, Thomas R. Hellier, Jr., David Maxwell, Donald Moore, Clyde A. Wilson, Jr., Melba C. Wilson, and Louis E. Vogele.

We are grateful for the cooperatiton afforded the project in Georgia by the United States Navy (Naval Air Station, Glynco) in granting us permission to make reconnaissance flights in their airships.

David Gould, Director of Coastal Fisheries for the Georgia Game and Fish Commission, generously allowed us to take part in patrol flights by the Commission airplane. We wish to thank the pilot, Clifford G. King, for his cooperation in facilitating our observation during the flights.

We are particularly indebted to Agents Robert Kilby and Robert S. Pfister, respectively of the Georgia Game and Fish Commission and the Florida State Board of Conservation, for their untiring co-operation in the field. Officials of the two agencies were most helpful in granting us collecting and study permits.

William W. Anderson furnished us with valuable unpublished notes on Georgia sea turtles.

Seton H. Thompson and Richard T. Whiteleather of the United States Fish and Wildlife Service Bureau of Commercial Fisheries, and W. L. Towns and E. S. Jaycocks of the Bureau of Sport Fisheries and Wildlife were especially helpful in making available the unpublished reports of work done at Cape Romain, South Carolina.

For their critical examination of the manuscript we wish to thank Mr. Anderson and Jack W. Gehringer.

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III. THE LOGGERHEAD TURTLES OF CAPE ROMAIN, SOUTH CAROLINA[11]

Abridged and annotated by DAVID K. CALDWELL

FOREWORD: After the first manuscript in the present series was finished and submitted for publication, and after the field work for the second study was completed and the data partially processed, general inquiry revealed a manuscript dealing with loggerheads, dated 1940, in the files of the Regional Office of the United States Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife, Atlanta, Georgia. This manuscript, resulting from Service-sponsored research (then the Bureau of Biological Survey) by Service personnel, has been made available for publication now through the efforts of Seton H. Thompson, Richard T. Whiteleather, and William W. Anderson of the Bureau of Commercial Fisheries, and W. L. Towns and E. S. Jaycocks, of the Bureau of Sport Fisheries and Wildlife.

Although many of the findings presented in the 1940 report have been published independently by subsequent workers (almost surely without knowledge of the report), and although some of the topics are covered in the first two papers in the present series, it was felt that so much of the material represents completely new data that judicious trimming would produce a valuable contribution—one somewhat overlapping, but complementary, to work completed later. Because I was actively involved in field research on the loggerhead turtle and had knowledge of its natural history, it was felt that among those Service personnel interested I might be best qualified to develop the report into a publishable paper that would not overly duplicate findings already or soon to be published.

It should be emphasized that all of the field work was done by William P. Baldwin, Jr. and John P. Lofton, Jr., or by those they acknowledge, and that the report which came to my hands is entirely theirs. I have deleted parts that are repetitious with other studies, have added later literature citations and limited data from my own findings where appropriate (so indicated), and have redrawn those of their figures retained to conform with Bulletin style. In some instances I have rewritten sentences for smoother continuity where parts were deleted. For the most part the wording has been left as it was in their original report. I hope that in no place have I changed Baldwin and Lofton's meaning. "We" or "our" refer to Baldwin and Lofton. The 1940 manuscript has been returned intact to the Bureau of Sport Fisheries and Wildlife Regional Office in Atlanta, Georgia, where it is now on permanent file.

David K. Caldwell.
March, 1959

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[11] Contribution number 44 from the United States Fish and Wildlife Service Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia, and a contribution from the United States Fish and Wildlife Service Bureau of Sport Fisheries and Wildlife.

SYNOPSIS: Detailed field studies show that Atlantic loggerhead sea turtles, *Caretta caretta caretta* (L.), make exploratory crawls to the beach during nesting season, and the fact that a turtle is on the beach does not necessarily mean she will nest at that spot, although she apparently will nest in the immediate vicinity on the night she explores, or very shortly thereafter.

Evidence, contrary to popular beliefs, shows no correlation between nesting activity and the stage of the moon, tide, and weather conditions. The physical features of the beach are apparently the most important factors in determining degree of nesting activity.

The nesting procedure in South Carolina is consistent with that noted in other populations throughout the species' range.

Details of the nest and of the eggs, their incubation, and hatching are presented for future comparison with other species. An average period of incubation of 55 days is demonstrated in South Carolina, and a growth rate is given for the embryos. Many hazards, such as numerous kinds of predators, roots of vegetation, and unfavorable conditions of temperature and moisture are shown to exist for the eggs and hatchlings, resulting in a high rate of mortality.

Considerable variation in size, color, and body form is demonstrated for hatchling loggerheads.

Although South Carolina lies near the northern boundary of the nesting range of the Atlantic loggerhead sea turtle, *Caretta caretta caretta* (Linnaeus), the turtle nests abundantly there. This is especially true for the beaches of the Cape Romain Migratory Bird Refuge (McClellanville, South Carolina) where over 600 nests are made each season. This refuge, also a haven for bird colonies of many species, consists of three low barrier islands and the acres of salt marsh (*Spartina alterniflora*) which lie between them and the mainland. [Similar conditions exist in Georgia at the Jekyll Island rookery discussed by Caldwell, Carr, and Ogren, 1959, herein—D.K.C.]. The South Carolina islands, known as Cape Island, Raccoon Key, and Bull's Island, possess about 19 miles of ocean beach, most of which is potential nesting ground for the loggerhead. Bull's Island is wooded but Cape Island and Raccoon Key are not. The dune vegetation on all three is very similar. The commonest plants that grow there are beach oats (*Uniola paniculata*), cord grass (*Spartina patens*), and beach tea (*Croton punctatus*).

As far as we can ascertain, the loggerhead nests on the Cape Romain beaches in greater numbers than anywhere else on the Carolina coast. Cape Island with 5 miles of front beach has 400 nests a season; Raccoon Key with 8 miles has an estimated 200 nests; and Bull's Island, about 6½ miles long, has approximately 30 nests.

Work at Cape Romain

For several years notes on the loggerhead have been kept by personnel of the Cape Romain Refuge. In the summers of 1937 and 1938, under the direction of Andrew H. DuPre, Refuge Manager, Lofton worked on the north end of the refuge, and in 1938 Baldwin worked on the south end. During the summer of 1939 a more intensive study of loggerhead nesting was conducted, the writers [Baldwin and Lofton—D.K.C.] staying full time at Cape Island. Although most of this report is based on our 1939 work, we have drawn from the notes of our previous work, notes of Mr. DuPre, and from unpublished information contributed by the Charleston Museum staff and other local observers. Grateful acknowledgment is made to these persons for their helpful suggestions and material.

Size of Mature Females at Cape Romain

[Baldwin and Lofton made measurements and recorded weights of a few loggerheads at Cape Romain. The mean carapace length for 18 turtles was 36½ inches, with a range of 33¼ to 40½. These results compare favorably with those made at Jekyll Island in 1958 and reported by Caldwell, Carr, and Ogren, (1959, herein). Baldwin and Lofton found the following relationship between weight and carapace length: 33¼ inches in carapace length, weight 193 pounds; 35¾, 218; 36½, 262; and 39, 298. Another individual with a carapace of approximately 35 inches weighed 257 pounds. Baldwin and Lofton report a skull in the Charleston Museum (catalog number 2373) reportedly taken from a South Carolina loggerhead turtle that weighed 607 pounds. They also state that a McGowan Holmes of Edisto Island, South Carolina, reported to the Charleston Museum in 1935 that the largest loggerhead of the many he had observed in that section had a carapace measuring 48 by 38 inches.—D.K.C.]

Length of Stay by Turtles at Cape Romain

In March the adult turtles appear in the bays and salt creeks which wind through Romain's marshes in all directions. Although previously they had been seen early in March, the first appearance recorded in 1939 was on 28 March. The first mating pair was observed in Cape Romain harbor on 31 March. It is during April and May that the turtles appear most frequently in the bays and creeks behind the islands. During this time mating couples are seen commonly, and often several males may be observed following or even clasping the same female. The latest recorded mating in 1939 was on 11 May, although it certainly was not the latest occurrence. In that summer, egg-laying commenced in the middle of May. During June, July, and August, when the adult females are laying on the front beaches, turtles are not commonly seen in the creeks, and we have no records of mating in those months. By October most of the adult turtles have disappeared.

Mating

We have records of mating for every hour from dawn to dark. Night mating doubtlessly occurs, but we have no information on the duration of copulation. As is the case with other species of marine turtles, paired loggerheads may copulate for extended periods and perhaps the females remate after each nest is made.

Mating turtles float in the water with the male in the superior position. While the female is submerged completely, the highest part of the male's carapace is usually out of the water. The head of the male emerges for breathing every few minutes, and the female struggles to the surface for air about every 5 minutes. With his plastron on the female's carapace, the male holds immovably to her with all four limbs, thus leaving the female free to swim. The very large tail of the male, which is 8 inches or longer, bends down pressing the cloacal opening against the similar organ of the female, and the two are tightly joined.

Nesting

Duration of Nesting

On Cape Romain's beaches nests are made from mid-May to mid-August. When work was begun at Cape Island on 19 May 1939 a few nests had already been made. The last nest was made there on the night of 18 August. Thus the laying season extended over a period of 3 full months with its peak in June and July. [A similar season was found at Jekyll Island, Georgia—D.K.C.].

Nesting and Non-nesting Crawls

The crawling of the turtle on the beach does not necessarily signify that the animal has made a nest. If the site does not appear favorable, the turtle often returns to the water without laying and usually tries again farther down the beach. In our counts we differentiated between nesting and non-nesting crawls. Each morning we patrolled the entire 5 miles of beach and recorded the preceding

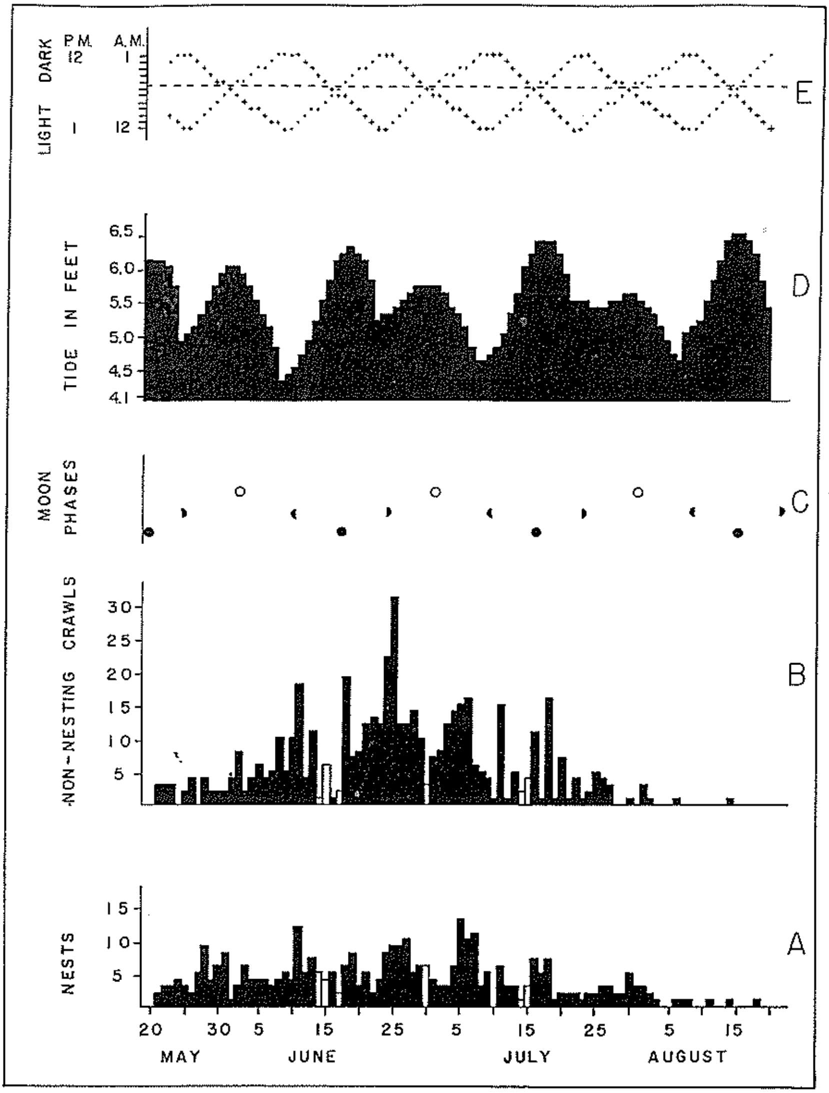

Figure 21.—Nightly number of loggerhead turtle crawls with correlated tidal and lunar conditions at Cape Romain, South Carolina, in 1939. The dates apply to all sections of the figure. Section A represents the total number of nests made each night (solid bars indicate total counts, open bars indicate that all crawls may not have been recorded for that date); Section B represents the total number of non-nesting exploratory crawls (bars as in A); Section C represents the phases of the moon, with solid symbols indicating new moon and open circles full moon; Section D represents the highest P. M. tides for the date; Section E represents the time, to the closest hour, of high tide (+ represents A.M., ° represents P.M.; symbols above the dashed line represent dark hours, those below indicate daylight hours).

night's nesting and non-nesting crawls. This information is presented in Figure 21. Complete data for the first few days on the island are not available and the information presented starts on 21 May. Except for the nights indicated, the nightly number of crawls is complete; those thus marked indicate that extremely high tides and blowing sand may have obliterated some of the crawls before we reached them.

The greatest number of nests made on any night was 13, and the nightly average for the 90-day period was 3.8. The greatest number of non-nesting crawls made on any night was 31 and the average (90-day) was 5.3. As is indicated in the figure, there is a fairly close correlation between the nightly numbers of nesting and non-nesting crawls.

Correlation of Crawls with Lunar and Meterological Data

Also included in Figure 21 are the daily records of tidal and lunar phases which would possibly affect nesting activities. These will be discussed separately.

Moon phase. It is a common local belief that the greatest nesting activity occurs during the period of the full moon. In Figure 21 the moon phases are diagrammed in relation to the number of crawls, and we can find no correlation to justify this belief. The peaks of egg-laying occur during all phases of the moon, and such peaks appear to be about 10-13 days apart.

Monthly range of tide. Assuming that turtles can hold their eggs for short periods, one might imagine that most turtles would put off laying until that time of month when tides are highest. In this manner they could utilize the higher water to float in nearer to the dunes. As Figure 21 shows, however, there was no correlation between height of tide and egg-laying. In that section the tides given are those which occurred from 12 noon to 12 midnight and are projected tides presented in the Coast and Geodetic Survey tables (1939).

Time of high tide. As loggerheads begin their nightly crawling just at dark, one might assume that most turtles would lay on those nights when the high tide, regardless of its height, was reaching its peak just at dark. No such correlation was found.

In speaking of the Bermudian sea turtles in general, Babcock (1937) mentions that they come ashore to deposit their eggs on a rising tide. McAtee (1934), in writing of the loggerhead (apparently in Georgia and other southeastern states), also mentions that the females come ashore chiefly on the rising tide. At Cape Romain, however, the loggerheads started coming ashore just after dark whether the tide was high or low, and most of the activity was in the first 4 or 5 hours after dusk. This information was gathered by nightly patrols of certain stretches of beach and rechecked on the morning patrol.

Other factors. Although no barometric readings for the Cape Romain area were available, comparison with Charleston data indicated no correlation. The nesting of turtles was little affected by minor storms or even easterly squalls. In one instance, however, on the night of 10 July, a severe thunder storm which started just after dark and was followed by an all-night rain may have been responsible for the lack of turtle activity; no nests were made that night and only one non-nesting crawl was observed, although there was much activity on the preceding and following nights.

The highest daily air temperatures throughout the laying season ranged between 81° F. and 97° F. The lowest daily temperatures ranged between 66° and 79°. There was no correlation between air temperature and nesting activity. Likewise, there was no apparent relationship between wind direction or velocity and turtle crawling.

Selection of Nesting Sites

The Cape Island beach during the summer of 1939 offered six kinds of potential nesting sites to female turtles. Figure 22 shows these beach types in cross section and we have given them descriptive titles:

A. *Truncate dunes*: Sharply eroded dunes backing a beach 5 to 10 feet wide on an average high tide. Extremely high tides pounded the base of these dunes. Turtles never were able to ascend the face of these, although they often tried. The truncate dunes graded into the next type.

B. *Ledge section*: A stretch of beach that had a ½- to 3-foot ledge breaking the middle of its natural slope. This type was variable and was formed by the action of wind and tide. At times the ledge was high enough to prevent the turtles reaching the dunes to nest [see Caldwell, Carr, and Hellier, 1956.—D.K.C.].

C. *Wide sloping beach*: 25 to 40 feet wide from average high tide line to base of dune. The outer dune was a continuous ridge which paralleled the ocean front and was broken in only a few places. Turtles could easily crawl from the surf to the base of the dunes.

D. *Narrow flat beach*: 10 to 20 feet wide and backed by small separated dunes. Turtles could often climb these dunes or go through the gaps between them.

E. *Wide flat beach*: Similar to the narrow flat beach, 30 to 50 feet wide and backed by small isolated dunes.

F. *Barren areas*: Stretching 100 to 400 feet back from the crest of the beach, with only traces of vegetation or low dunes to break their flatness.

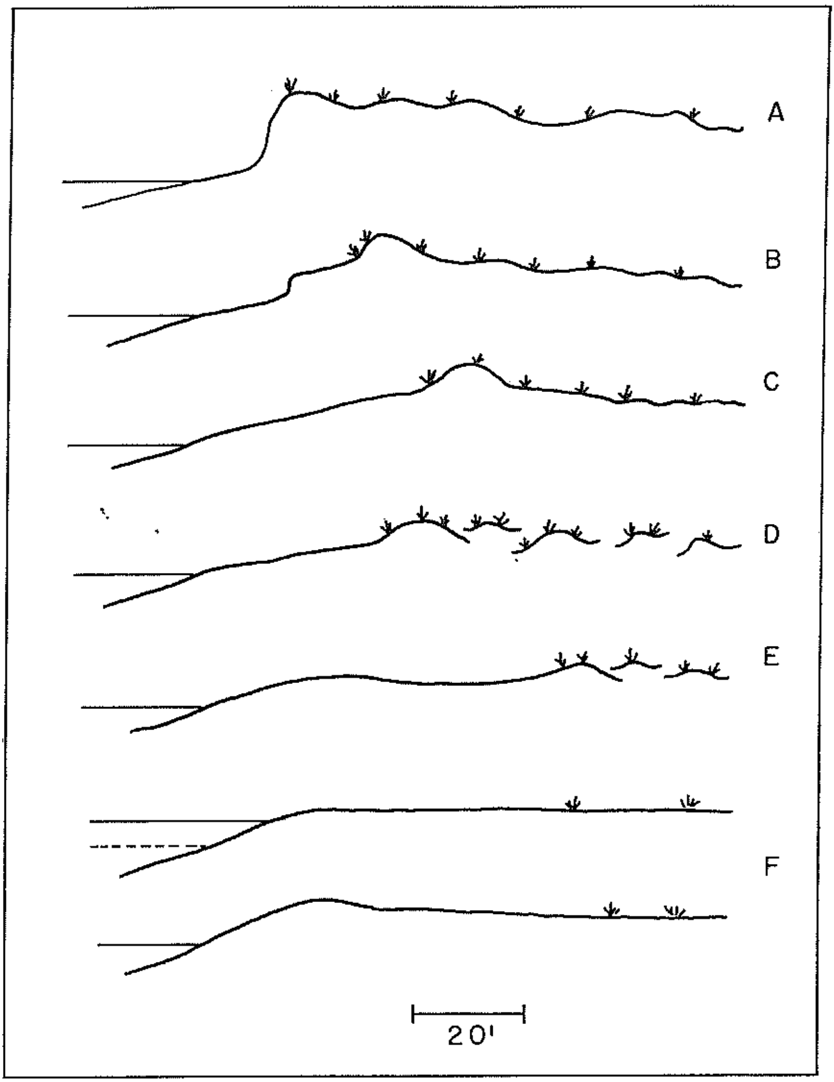

Figure 22.—Diagramatic cross sections of beach types at Cape Island, South Carolina, in 1939. See text for details.

The Cape Island beach, in general, is much narrower and steeper than those of Raccoon Key and Bull's Island, and the sand is coarser. The beach at Cape Island is by no means stable, but is constantly cutting away and building up. Remains of nests made in 1938 were noticed in 1939 to be on top of truncate dunes 15 feet high, which indicated considerable cutting away during the winter between these two nesting seasons. Observations in the first part of the summer of 1940 show that the beaches have changed again. In fact, the truncate dunes of 1939 have been changed into a wide sloping beach of 1940 by the deposition of sand at their base so this stretch of beach which was so unsuited for turtle nesting in 1939 is an ideal type in 1940, and contains an abundance of crawls.

Just as certain types of beach appeared to our eyes more favorable than others for nesting, so did they to the turtles. Data to substantiate this, based on the location of 343 nests and 463 non-nesting crawls, are offered in Table 3.

Some of the most interesting facts that can be deduced from the information presented in Table 3 are those relating to turtle behavior in selection of nest sites. What process of thinking makes a turtle leave the truncate dunes without nesting and swim farther along the shore to nest on the wide sloping beach? Such things happened. In the truncate dunes one nest was made every 197 feet of ocean front and one non-nesting crawl every 32 feet; for every turtle that laid on this low beach, six turtles returned to the surf without laying. On the high wide sloping beach, however, turtles made one nest every 28 feet, and one non-nesting crawl every 55 feet. For every turtle that nested, a theoretical half of a turtle returned without nesting. Thus this high type of beach backed by rounded dunes (see Figure 22) was chosen by turtles more often than any other type. With its 1 nest every 28 feet, compare it to the barren area with its one nest every 204 feet. This is further evidence that low dunes backing a high beach increase its desirability as a nesting site.

Other factors, such as the amount of moonlight, probably influence the turtles in selecting various types of beach, but to what extent we do not know. Statistical data, which will not be presented here, indicated that throughout the season there was no important shifting of turtle nesting from one type of beach to another. [Aerial reconnaissances of all of the beaches of Georgia and most of those of North Carolina, South Carolina, and the Atlantic coast of Florida have indicated that nesting turtles show a preference for a beach backed by high dunes or vegetation, which thus presents a dark and broken

TABLE 3

NUMBER OF NESTING AND NON-NESTING CRAWLS MADE BY ATLANTIC LOGGERHEAD SEA TURTLES ON EACH TYPE OF BEACH AT CAPE ISLAND, SOUTH CAROLINA, IN 1939.

Beach Type	Percent of total beach	Total feet of beach	Number of nests	Number of feet of beach per nest	Number of non-nesting crawls	Number of feet of beach per non-nesting crawl	Number of feet of beach per both types of crawls	Ratio of nesting crawls to non-nesting crawls
Truncate Dunes	7.0	1970	10	197	61	32	28	1 to 6.1
Ledge Section	7.9	2223	40	56	61	36	22	1 to 1.5
Wide Sloping	11.0	3096	110	28	56	55	19	1 to 0.5
Narrow Flat	7.8	2195	55	40	62	35	19	1 to 1.1
Wide Flat	16.3	4587	59	78	38	121	47	1 to 0.6
Barrens	50.0	14071	69	204	185	76	55	1 to 2.7
TOTAL	100.0	28142	343		463			
AVERAGE				82		61	35	1 to 1.4

horizon to a turtle in the water instead of the lighter and relatively unbroken outline offered by sand flats or the open ocean. This may be one factor in drawing the turtles to such beaches. To turn seaward or along the shore to the light, unbroken, horizon would of course be disadvantageous to a turtle trying to land to nest. The apparent hesistancy for a turtle to strand on a barren flat may be a secondary result of this same phenomenon of relation to horizon, rather than some physical factor of the barren beach itself.

In an analysis of distance crawled by nesting and non-nesting females in relation to the type of beach, Baldwin and Lofton found that the turtles prefer to nest on high beaches near or in the dunes, beyond the reach of the tide. In addition, on large barren sand flats where turtles may crawl hundreds of feet back from the ocean, they prefer to lay only 1 to 30 feet from the crest. They found that adult turtles crawling far back on these barrens often became confused and wandered hundreds of feet in all directions before locating and reentering the ocean. Therefore, nesting close to the ocean not only guarantees a safer journey for the young when they hatch, but also insures the adults' safe return to the surf.—D.K.C.]

Primary Excavation

When the turtle finally has selected a desirable nesting place, she makes a primary excavation. This is a shallow depression, larger than or approximating the size of the turtle, made by the turtle's movements. The turtle moves the posterior end of its body from side to side and pushes the sand out with its hind flippers, often making the middle of the excavation a foot deep. This primary excavation is largely exploratory, and often the turtle will move on farther and dig again if the site does not suit her. Turtles made this primary excavation in 23 percent of their non-nesting crawls; in the best type of nesting site, the wide sloping beach, it was made in 46 percent of the non-nesting crawls. In the truncate dunes, one of the least desirable sites, it was made in 13 percent. In short, those beach types that had the most nests per unit of ocean front likewise had the most investigation, as indicated by primary excavations by non-nesting turtles. Several factors are responsible for the abandoning of these primary depressions. An obvious one had to do with the conditions affecting digging, namely: sand packed too hard, sand too dry and soft, layers of oyster shells, and an abundance of tough vegetation roots. Another factor was position in relation to tide, for sites well above the average tide level are preferred. [It is presumed, though not stated, that all nesting females made the primary excavation as was the case during 1957-58 studies on the Jekyll Island rookery.—D.K.C.]

Secondary Excavation

[Here Baldwin and Lofton cite the work of others as being representative of their own findings. An illustrated description of the process is presented by Caldwell, Carr, and Ogren, (1959, herein). One comment by Baldwin and Lofton, also noted on several occasions at Jekyll Island in 1958, concerns repeated secondary digging by a turtle. They state that just as the hardness or the caving in of the sand or the presence of vegetation roots affect the primary excavation, so do they often cause the turtles to cease digging the egg hole. In one site examined, the female had dug eight holes and still had not laid her eggs.—D.K.C.]

Laying and Covering the Eggs

[This process, while described by Baldwin and Lofton, has been discussed in detail and illustrated by Caldwell, Carr, and Ogren (1959, herein).—D.K.C.]

Return to the Sea

After covering the nest, the turtle is ready to return to the sea. Of the 350 nest sites examined, in only one instance did we find that a turtle had paused on the return crawl to make excavations similar to those normally made before digging the egg hole. In returning to the sea the female is somewhat exhausted and usually makes frequent stops to rest. One turtle that had not been disturbed crawled the 180 feet to the sea in 25 minutes. Another undisturbed turtle traveled the 50 feet to the surf in 3 minutes. The strength of these turtles is illustrated by the fact that one which had just finished laying carried two of us to the ocean on her back—a weight of about 275 pounds.

Not infrequently turtles nesting at Cape Romain became lost on the return to the sea. This occurred on two types of beaches, flat barren areas and those backed by isolated dunes. These barren areas, from 200 to 400 feet across, gradually slope back from the crest of the ocean beach making the ocean invisible to a turtle 50 or 60 feet inland. One turtle, after making four primary excavations, moved inland, became lost, and wandered extensively for 2,140 feet over the sandy flat. Another turtle, also on a barren area, apparently made several small circles after nesting to determine her position with respect to the sea before she returned to the water. A third individual nested well back from the crest of the beach in the barren area, and on completing her nest crawled diagonally back to the crest of the beach to a point where she could see the beach. For some undetermined reason she then reversed her direction and crawled for several hundred more feet around the barren area before returning to the water. Such action was most unusual. A fourth turtle became confused among a group of isolated dunes. She nested on the top of a 10-foot dune 100 feet from the ocean. Upon descending the dune, she could not see the ocean and wandered extensively among the 2- to 5-foot dunes, never climbing any of them, until eventually she reached the safety of the ocean beach. An occasional loggerhead skeleton far back among the dunes is mute evidence that turtles do remain lost until the merciless heat of the rising sun kills them.

Description of the Nest

Position of the Egg Deposit

When the laying turtle has returned to the sea, its tracks lead to a nest site that is easily recognized by the churned up sand and crushed vegetation. This area, if located in dune vegetation which hampers the movements of the turtle, is usually circular and 4 or 5 feet in diameter. In sites lacking plant growth, the muddled areas are oval to oblong, and may reach a size of 6 by 25 feet. The exact position of the nest in all this muddling may appear difficult to locate, but with a little practice one can soon pick out the exact spot. To us it appeared that the egg deposit was usually near the fore, or entrance, edge of the muddling and equidistant from either side.

Depth of Eggs

The cavity the eggs fill is 6 to 10 inches deep, 8 to 10 inches wide, and slightly wider at the bottom than at the top. This egg deposit is found at varying depths. The depth of the top eggs in 317 nests ranged from 5 to 22 inches, with two-thirds of them between the 11- and 16-inch levels. This agrees with the depths of six North Carolina nests measured by Coker (1906). As already mentioned, fresh nest sites in open sand present a different appearance from those in dune vegetation, and it was thought that the depth of the egg deposits might correspondingly be affected. Distribution of the data according to the various degrees of cover, however, revealed only a slight tendency for nests in the dune vegetation to be a bit shallower than those on the edge of vegetation or on open beaches. The extreme depths were reached only by turtles making unusually deep primary excavations, and egg holes as deep as possible, with the eggs covered by sand to an extraordinary height. In conclusion it might be mentioned that the egg deposits laid at the last of the season were buried just as deeply as those first laid. Furthermore, there was no apparent correlation between the depth of the eggs and the chances of sand crab depredation (see below).

Sand Conditions

The sand piled over the fresh egg deposits is usually reduced 1 to 2 inches during the incubation period by wind and tide action. Obviously this erosion and subsequent obliteration of the site decreases the chances of nest depredation.

The sand over the nest, as left by the turtle, is firmly packed immediately above the eggs and loosely piled above that. As incubation proceeds and the eggs settle, an air space often forms between this packed sand and the top eggs. Many times, by the time the young turtles have hatched, this space has grown to be a small domed chamber. If the arch of this chamber collapses and the sand falls upon the eggs or young, a small but noticeable surface crater results. This probably is easily found by foraging sand crabs [or raccoons—D.K.C.] to the detriment of the nest.

Eggs

Number Laid

A study of 71 nests throughout the laying season revealed clutch sizes ranging from 64 to 198 eggs, with an average of 126.

Six nests examined by Coker (1906) in North Carolina contained 118 to 152 eggs. Alexander Sprunt, Jr. has checked the number of eggs in loggerhead nests for many years in the Charleston section. His three highest counts were 180, 219 (Raccoon Key), and 341 (Sullivan's Island). Marshall Alston, a negro fisherman who formerly collected and sold the eggs from hundreds of Cape Romain nests, reported that the smallest clutch he ever found contained 65 eggs and the largest 280.

Relation Between Number and Time of Season

Several authors have pointed out that it was "believed" that the loggerhead laid several clutches a season, the number of eggs per clutch decreasing each successive time. [It has now been shown (Caldwell, Berry, Carr, and Ragotzkie, 1959, herein) that individual loggerheads do nest several times a summer.—D.K.C.] We have analyzed the clutch size for 71 Cape Romain nests according to the time of season laid. It appears that the number of eggs does decrease as the season progresses. [A similar analysis of 26 clutches at the Jekyll Island rookery in 1958 produced the same results.—D.K.C.].

Size of Eggs

The measurement of 827 eggs taken from 44 nests the day after they were laid revealed that the greatest diameter of normal eggs ranged from 35 to 49 mm., with an average of 41.5 mm. Loggerhead eggs, when laid, appear perfectly round. Many of the measurements were secured by measuring only the 5 top eggs in each nest. This sampling avoided handling of whole clutches and the subsequent effect on percentage of hatch. Some nests were completely excavated and the entire clutch measured and weighed. The total weight of 119 eggs in one nest was 4,155 grams, or an average weight of 35 grams per egg. The variation of egg diameter within a clutch ranged from 3 to 11 mm.

Size of Eggs in Relation to Order Laid

Further investigation of egg size variation revealed that, within the clutch, the eggs laid last were smaller than those laid first. This was determined by the measurement of six freshly-laid clutches. The resulting data are presented in Table 4. The eggs were measured as they were removed from the nest and each group of 20 is composed of eggs deposited in the same layers and within the space of a few minutes or, in short, in the order that they left the female's body. The groups of 20 are arranged in the table with the eggs found in the top of the nest (laid last) at the top of the column, and in descending order through the nest to those in the bottom (laid first).

That the eggs laid last would be smaller than those laid first seems natural if one considers their relative position to the many undeveloped eggs that remain in the turtle's egg tubes. All these measurements were made the morning after each nest was made and the possibility of nest pressure affecting these diameters may be largely disregarded for the eggs were in no way misshapen. Moreover the range of variation within each layer was additional evidence that the size differential was natural.

Eggs of unusual sizes are occasionally found in nests. Small yolkless eggs 28 to 30 mm. in diameter are one type and may represent the last eggs laid by a turtle. On the other extreme, abnormally large eggs are occasionally found. One egg, almost hen-egg shaped, measured 51 by 43 mm. when laid. Another, with two yolks, measured 66 by 47 mm.

TABLE 4

RELATION OF EGG SIZE TO ORDER OF LAYING IN THE ATLANTIC LOGGERHEAD SEA TURTLE AT CAPE ROMAIN, SOUTH CAROLINA, IN 1939. MEASUREMENTS ARE THE AVERAGE DIAMETERS IN MILLIMETERS.

Relative position of eggs in nest	Nest Numbers					
	294	295	322	331	337	346
20 laid last (top of nest)	39.8	37.7	40.4	41.4	45.1	43.8
20	40.6	38.4	40.6	42.6	45.7	44.3
20	41.2	38.8	40.7	42.7	45.9	43.9
20	42.3	39.2	40.7	42.7	45.4	43.9
20	43.6	39.4	40.7	43.1	—	44.0
20 laid first (bottom of nest)	—	40.2	40.9	—	—	—
Average diameter	41.5	38.9	40.7	42.5	45.5	43.9

Egg Size in Relation to Adult Size

A definite correlation between the size of the eggs laid and the size of the turtle was noticed. In seven instances in which the carapace lengths of the adult turtles and the average diameters of their eggs were known, it was found that the larger the turtle, the smaller the average size of her eggs.

INCUBATION

Development of the Embryo

From embryo measurements secured through periodic examination of two nests, a composite growth curve has been constructed (Figure 23). Macroscopic examination of opened eggs revealed no embryos for the first 2 weeks, but on the 14th day embryos about one millimeter long were observed in several eggs. From then on growth was rapid. When examined on the 26th day the embryos were pale grayish blue and showed movement, and by the 32nd day they were very active and their eyes were open. Fifty-four days elapsed between the night of egg-laying and the appearance of the turtles on

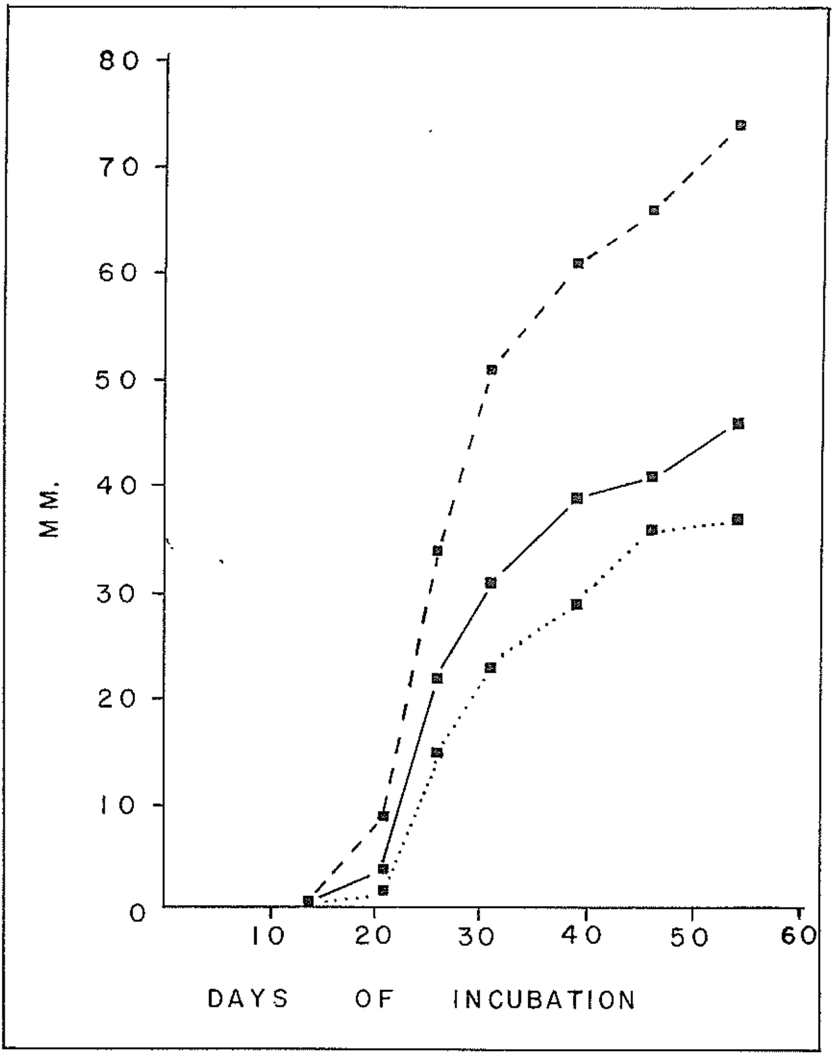

Figure 23.—Composite growth of loggerhead turtle embryos from two nests at Cape Island, South Carolina, in 1939. Dashed line represents total length, solid line represents carapace length, dotted line represents carapace width. The average diameter of the five top eggs when laid in each nest was 41 mm.

the beach. Hatched and developed turtles, however, were down in the egg deposit on the 51st day and perhaps earlier.

During incubation one of the most obvious external changes that occurs is the "whitening" of the egg shells. When deposited, the creamy white eggs are bathed in a clear secretion which causes them to glisten. This soon evaporates and the shells gradually whiten. Several nests made in August were examined periodically and it was found that on the second day of incubation the majority of the eggs throughout the deposit had small round white marks on their "tops", with a few eggs having them on the sides, and none on the under surface. By the end of the first week of incubation the whitening of each shell was three-fourths to nine-tenths complete, and was proceeding at the same rate for all depths of the egg deposit. At this stage the small remaining unwhitened areas were all on the under surfaces of the eggs. By the end of the second week the shells were completely white, and this probably had occurred about the 10th or 12th day. This drying and hardening of the egg shell, which proceeds uniformly regardless of the location in the egg deposit, points to a uniform heat distribution and incubation rate throughout the nest. The shells of infertile eggs do not whiten in this manner, but by the end of several weeks have acquired a deep creamy color.

Another obvious change is the gradual swelling of fertile eggs as incubation proceeds. The absorption of soil moisture is responsible for this. The total length of the fully developed embryo just before hatching is greater than the largest diameter of the freshly laid egg.

Incubation Time

The length of incubation was considered to be that period beginning with the egg laying and ending with the appearance on the surface of the main group of young turtles. For 55 Cape Island nests this ranged from 49 to 62 days, and the average period was 55 days. [Caldwell, Carr, and Hellier (1956) found incubation periods in Florida as long as 68 days under somewhat unnatural conditions of handling and habitat—D.K.C.]

Factors Affecting Incubation

Some half dozen factors might be considered as possibly affecting the incubation length: Sunlight and shade, nest temperature, depth of egg deposit, soil type, moisture content of the soil, and tidal and underground water level conditions.

Sunlight and shade. Incubation periods of nests made at the first of the laying season (last of May) and those made at the last of that season (last of July) were found to be longer than those for nests made in the middle of the season. This, it was felt, was due to the total amount of heat received by these nests. This heat factor depended upon possible hours of sunlight, the actual hours of sunlight, and the range of air temperature. Data for the Charleston area supplied by the U. S. Weather Bureau indicate that the possible hours of sunlight at the start of the laying season (middle of May) was 14 hours per day, rising to 14.3 through June, and gradually dropping to 12 hours by the end of September (practically the incubation season). The actual hours of sunlight, however, were much lower than the possible hours: 64 percent in May, 60 percent in June, 75 percent in July, 61 percent in August, and 57 percent in September. The average daily air temperature was closely correlated with the actual hours of sunlight, those periods experiencing the most sunlight also having the highest temperatures. The temperatures through the last of June, July, and first of August averaged higher than those at the first and last of the incubation. In short, incubation periods shortened as the temperature and amount of sunlight increased.

Additional information on the relation of incubation length to the amount of sunlight is supplied by the following observation by Mr. Chamberlain of the Charleston Museum. He collected 12 eggs from a nest made on Cape Island on 6 June 1927. Placed in a box of sand, these eggs were kept in a warm garage and occasionally sprinkled with water for 2 weeks. They were then removed to a location where they received 2 hours of sunlight daily. On 16 September, 102 days later, the eggs were uncovered and it was found that, of the two hatched turtles, one was still alive and of normal dimensions. This extreme length of incubation caused by unnatural conditions was no doubt largely due to the absence of sufficient sun heat.

Under natural conditions shading is caused by dunes and thick vegetation. In analyzing the incubation lengths of specific nests in relation to natural conditions of sun exposure, tide, and depth of egg deposit, it was found that for the most part the data further illustrated that the incubation period varies with the amount of sun heat.

Nest temperature. As determined by a fairly extensive series of thermometer readings taken under all conditions of weather, the temperature within the nest is subject to less fluctuation than the surface temperature. Thus, while our extremes of daytime surface temperatures ranged from 74° to 128° F., the temperature within the egg deposit fluctuated only from 77° to 93° F. In fact, the egg deposit temperature usually remained between 82° and 88°, and the 77° reading was recorded only after a 3-day rain. The constancy of temperature within the nest was maintained not only during the day but also at night, even though the surface temperature might then fall considerably. The maintenance of a stable temperature appears to be a requirement for a normal incubation length. Of course the temperature decreases with an increase in the depth at which readings are taken, but in the normal depth range of loggerhead nests this is a matter of only 1 or 2 degrees.

Depth of eggs. It will be recalled that at Cape Island there was considerable range of depth for eggs in different nests. To determine whether the depth of eggs affected the incubation length, one fresh nest was excavated and groups of eggs from all parts of the original deposit were reburied at varying depths under similar environmental conditions. On the 55th day of incubation the young were out of the eggs in all the levels from 12 to 30 inches. From the relative position of the young it may be assumed that those in the shallower depths hatched slightly before those in the greatest depths. Twenty-four hours later they had reached the surface from the shallowest deposits, but from the extreme depth they did not reach the surface until 8 days later. Therefore the depth does not greatly affect the actual length of incubation, but only the time required for emergence. It is of additional interest to point out that the young from the 12 smallest eggs in this clutch, which were buried together at the 15-inch level, were on the surface on the 54th day, or 2 days before the young from average-sized eggs at the 15-inch level had reached the surface. This may indicate that small eggs hatch before large eggs of the same clutch.

Soil type and moisture content. Two closely related factors that doubtless affect incubation are the soil type and moisture content. On the Cape Island beach the soil types varied from crushed oyster shell to fine sand. The latter is usually very dry. Three types of sand were assayed for moisture content. These samples, taken from below the surface, were typical of the majority of nest sites. The moisture contents were determined by Dr. Horatio Hughes of the Department of Chemistry of the College of Charleston, and are presented below:

1. Fine sand at the base of dunes in *Uniola paniculata* roots 1.3%
2. Beach sand at the base of truncate dunes 3.1%

3. Coarse sand from barren flats among isolated dunes 4.2%

The above figures are the percentages of moisture by weight. Sand taken from the site of one North Carolina nest by Coker (1906) contained 3.8% water.

Underground water level and tide. Although the layer of sand on the surface is dry as a result of evaporation, the sand a few inches below is damp, and this condition extends down to the underground water level. To the touch this sand is moist and cool when compared with that at the surface. On top of the dunes the upper layer of dry sand appears to be thicker than at the base of the dunes or on flats. In all of the above sites loggerhead nests experience normal incubation, and it appears that the optimum moisture content would be 2 or 3 percent. In nests in low areas where the tide not only can cover the nests frequently but also raise the underground water level around the eggs, the incubation period is lengthened. In one Bull's Island nest so situated in 1938, the sand was so wet that earthworms (*Lumbricus*) were found in the deposit, and the incubation period, as based on the only turtle that hatched, was 80 days. The effect of water on the percentage of hatch will be discussed later.

Hatching

Escape from the Egg

As the end of the incubation period nears, the eggs have increased considerably in size through the absorption of water. The curved embryo, which completely fills the egg, develops a sharp point on the snout just before hatching. The combination of the increased internal pressure and the use of the egg tooth facilitates the escape from the egg shell. The pipping and escape from the eggs occur in all levels of the egg deposit almost simultaneously. In one nest we examined the turtles were just pipping the eggs on the 48th day of incubation; they had egg sacs measuring ¾-inch by 1 inch, and their carapaces did not appear to be fully grown. On the 55th day the fully developed young, without trace of the egg sac, appeared on the surface of the beach. The shortest period of actual incubation we recorded was one in which the young were pipping the eggs on the 45th day. In general, the external egg sac has been completely absorbed shortly after the young have escaped from the eggs, although it may occur before this act has been completed.

Escape from the Nest

Internal egg yolk must nourish the small turtles during their upward struggle through the sand; while this climb of 1 to 2 feet may take only 1 day, the average time is 2 to 3 days, and not uncommonly as long as 5 or 6 days.

Young loggerheads usually appear on the surface at night, which prevents their being killed by the heat of the daytime sun. The intensity of heat is probably the factor controlling the time of this egress, for turtles found 1 to 4 inches under the surface in the middle of the day were inactive, but emerged in the cool of the following night. In the few instances where turtles reached the surface during the day they appeared stupified by the surface heat which soon kills them. Turtles removed from the depths of a nest during the day, however, and released on the beach easily reach the water before being affected.

Just as the turtles escape from the eggs more or less together throughout the nest, most of them arrive at the surface during the same night. Those climbing up first loosen the sand and make the way easier for the last of the hatch. Sometimes the escape from the nest will last a week, with the main emergence preceded or followed by successively smaller numbers.

Percentage of Hatch

The percentage of hatch, based on 62 nests, is presented in Table 5. The nests are divided into groups according to relation to tide exposure and presence of vegetation roots. Not only are the averages presented, but also the range of hatchability for each type. The range indicates that some nests will be highly unsuccessful no matter how favorable their location. The average hatch was 73.4 percent. Eggs that did not hatch were opened and examined macroscopically; some of those considered as having no development may well have contained extremely small dead embryos. As Table 3 shows, however, 20.7 percent of all eggs were infertile, and 3.8 percent contained embryos that died in various stages of development. One interesting discovery was that 5.3 percent of the eggs laid among *Uniola paniculata* were destroyed by its roots. The hair roots formed thick mats around the individual eggs, eroded the shells, and desiccated them; often the sharp-pointed stolons pierced the eggs. A small number of the turtles that pipped their eggs were unable to completely escape the shell and died. Still another small percentage escaped from the

TABLE 5

PERCENTAGE OF HATCH, BASED ON 62 ATLANTIC LOGGERHEAD SEA TURTLE NESTS UNDISTURBED BY PREDATORS OR EROSION, AT CAPE ISLAND, SOUTH CAROLINA, IN 1939. FIGURES REFER TO PERCENTAGE OF TOTAL EGGS IN CLUTCHES LAID IN EACH OF THE FIVE SITES (SEE TEXT FOR EXPLANATION OF TYPES OF BEACH).

		Open, Exposed Sites		Base of Dunes		On Dunes in *Uniola* roots	Average
		Occasionally covered by tide	Never covered by tide	Occasionally covered by tide	Never covered by tide	Never covered by tide	
Successfully hatched	Mean:	66.9	73.3	86.7	82.4	65.3	73.4
	Range:	29.0–97.0	30.0–95.0	82.0–92.0	16.0–98.0	31.0–96.0	
Embryos died in eggs	Mean:	5.7	4.3	3.4	2.1	3.0	3.8
	Range:	0.0–43.0	0.0–17.0	4.0–6.0	0.0–11.0	0.0–9.0	
No apparent development (sterile)	Mean:	26.3	20.8	9.7	14.5	25.5	20.7
	Range:	2.0–70.0	4.0–69.0	2.0–16.0	1.0–78.0	3.0–57.0	
Eggs destroyed by *Uniola* roots	Mean:	None	None	None	None	5.3	1.0
	Range:					0.0–42.0	
Young died in pipped eggs	Mean:	0.5	0.9	None	0.6	0.2	0.5
	Range:	0.0–2.0	0.0–4.0		0.0–2.0	0.0–2.0	
Young died in nest	Mean:	0.6	0.7	0.2	0.4	0.7	0.6
	Range:	0.0–2.0	0.0–3.0	0.0–1.0	0.0–3.0	0.0–3.0	
Total nests		13	19	4	14	12	62

shell successfully but were caught in the nest and died. This was caused by their inability to climb through the tightly packed deposit of hatched eggs or matted vegetation roots, or their tendency to burrow horizontally into hard sand instead of perpendicularly to the surface. In summing up the data this table presents, it may be said that those nests located at the base of dunes and rarely if ever covered by water are better situated than those on exposed beaches, especially those occasionally covered by tides, or on the vegetated dunes. As noted earlier in this paper, the female loggerheads selected sites at the base of dunes much more than in the other types.

The Hatchling

Size of the Young

A total of 398 young loggerheads from 31 nests were measured just after hatching. The carapace length ranged from 38 to 50 mm., with a mean of 45 mm.; the carapace width ranged from 31 mm. to 40 mm., with a mean of 35.5 mm.

The average weight of a newly hatched turtle, as determined from 104 specimens of one nest, is 21.2 grams. [These turtles are heavier than those reported by Caldwell, Carr, and Hellier (1956) from two localities in Florida—D.K.C.]

It was mentioned earlier in this paper that the larger turtles laid the smaller eggs, but whether a relationship exists between the size of the adult and young is not known.

Color of the Young

Newly hatched loggerheads have a wide range of color. The carapace varies from a yellowish buff through all shades of brown to a gray black. This coloration is by no means uniform, but lighter on the outer plates of the carapace. The plastron ranges from a pure creamy white to a gray black mottled with this white. Prominent points on the plastron are lighter than the grooved or flat areas. A light plastron is not necessarily correlated with a light carapace. Sometimes the individuals from a single nest have plastrons predominantly light or dark. These colors refer to those of wet specimens, for most dry specimens have a grayish cast.

Shield Variations

We examined 154 specimens from Cape Romain nests for variation in the number of costal shields [lateral laminae—D.K.C.], inframarginals, extra anals, and extra gulars—one pair of each of the latter two is the expected number. The results of this analysis are included as Table 6. Although not evident from the table, the young of some nests tended to have greater shield variation than those of others.

TABLE 6

SHIELD VARIATION IN YOUNG ATLANTIC LOGGERHEAD SEA TURTLES. DATA ARE BASED ON 154 NEWLY HATCHED SPECIMENS FROM CAPE ROMAIN, SOUTH CAROLINA IN 1939. ALL COUNTS ARE MADE VIEWING THE TURTLE FROM THE DORSAL ASPECT.

Right	Left	Number of Turtles	Percent of Total
		Lateral laminae	
5	5	144	93.4
5	6	7	4.5
5	4	1	0.7
6	5	1	0.7
4	4	1	0.7
		Inframarginals	
3	3	57	37.0
4	3	14	9.1
3	4	21	13.6
4	4	56	36.3
5	4	2	1.3
6	4	1	0.7
4	5	1	0.7
5	5	2	1.3
		Extra (more than one pair) anals	
None		134	87.0
Median		13	8.4
Right & Left		5	3.3
Right, Left & Median		2	1.3
		Extra (more than one pair) gulars	
None		93	60.3
Median		60	39.0
Right & Left		1	0.7

Abnormal Young

During this investigation a few specimens were found which might be termed freaks. One turtle that hatched and was otherwise normal had no external openings for the eyes. Another had no left front flipper. One pair of embryos was found attached to the same egg yolk, and although completely developed, the turtles were dead. In another instance an embryo having one head joined to two bodies also died before hatching. An unusually small turtle that hatched and was otherwise normal had a carapace measuring only 34 mm. by 25 mm. (expected measurements are 45 mm. by 35 mm.).

The most interesting abnormality, however, was the presence of white embryos in about 15 percent of 65 nests examined. Never more than 3 or 4 were found in one nest. These embryos, in all stages of development, ranged from blueish white in the younger forms to creamy white in the fully developed ones. The carapace, plastron, and skin of the animals were uniformly colored. None of these abnormal embryos hatched, but some were found fully developed and alive in the egg a week or more after the normal turtles of the nest had hatched. One was found that had pipped the egg and then died. This probably indicates that development of the white embryos requires a longer period than normal ones. In addition, this absence of color appeared to be linked with the presence of malformations of the jaws and eyes.

Enemies and Mortality

Enemies of Adults

Enemies of the loggerhead are numerous. Formerly many of the adults were slaughtered for food in this region, although the practice is now outlawed by South Carolina. Some references indicate that sharks also destroy the adults. We have a local record of dogs killing loggerheads. According to a note in the Charleston Museum files, T. B. Fitzsimmons found two dead turtles with torn necks on the Botany Bay Beach, Edisto Island, within a few days of each other in the summer of 1929. A few nights later he saw his two hound dogs rush down to the beach and attack an adult turtle. He stopped the dogs and found the same wounds as on the other two turtles.

Enemies of the Young

The young are subject to tremendous predation by fishes, sharks, sand crabs (*Ocypode albicans*), raccoons, gulls, and to a lesser extent by crows. Sand crabs, which cover the beaches at night, form a gauntlet that the hatchling turtles must run, and many of the defenseless loggerheads never reach the sea. While the larger crabs

TABLE 7

Fate of 343 nests of the Atlantic loggerhead sea turtle Cape Island, South Carolina in 1939. Figures refer to percentage of total nests per beach type.

	Truncate Dunes	Ledge	Wide Sloping Beach	Narrow Beach	Wide Beach	Barren	Total Nests	Average Percent
Hatched Successfully	None	27.5	27.2	67.2	49.1	63.8	151	44.0
Entered by crabs	10.0	35.0	60.9	29.0	35.6	30.4	140	40.8
Destroyed by raccoons	None	5.0	10.9	None	5.1	2.9	19	5.6
Washed away	90.0	32.5	1.0	3.8	10.2	2.9	33	9.6
Total number of nests	10	40	110	55	59	69	343	100.0
One nest per	197 feet	56 feet	28 feet	40 feet	78 feet	204 feet	82 feet	——

can easily carry the young turtles to their burrows and consume them, medium-sized crabs often have difficulty holding the struggling prey.

On 14 September 1931 according to a note in the Charleston Museum files, a young loggerhead was taken from the stomach of a "black-fish" (*Centropristes striatus*) and identified by E. B. Chamberlain. This fish was taken in 14 fathoms on "South Ground" off the Charleston bar. Interesting not only in its connection with predation, this also points to a possible migration of the newly hatched turtles to deep water. [See Caldwell, Carr, and Ogren (1959, herein)—D.K.C.]

Enemies of Eggs

Depredation of nests is very high in all parts of the loggerhead's range. McAtee (1934) says that nests of the loggerhead are pilfered by various enemies, but that the work of natural enemies is insignificant compared to the depredations of hogs, where they are present, and of man. At Cape Romain neither of these two predators is present, but depredations by sand crabs and raccoons are extensive. Table 7 presents the fate of 343 Cape Island nests. The data are tabulated for beach types and for the entire island. Only 44 percent of the nests hatched without being disturbed. Sand crabs entered 40.8 percent, although this does not mean that some of these nests did not later hatch some young.

Sand Crab. Crabs entered nests regardless of the stage of incubation and condition of the nest site. It is remarkable how these predators can locate an egg deposit after all surface signs of the nest have been obliterated. It may be largely accidental, or connected in some manner with the presence of the soft sand immediately over the eggs. Newly made nests still marked by the turtle's crawl are easily found by the crabs, which dig shallow 3- to 12-inch holes experimentally all over the site. This sometimes results in their finding the egg deposit. A nest that has been entered usually shows a hole surrounded by scattered egg shells. In soft sand this entrance hole may be gradually excavated to reach 1 foot in diameter instead of the customary 3 or 4 inches. The crabs, sometimes a dozen in the same nest, may either eat the eggs in the nest or remove them to nearby dunes or to their permanent burrows. Although only one crab may discover an egg deposit, sometimes a dozen more may move into the area within the space of a week and dig their burrows around the original one. The number of sand crabs on the Cape Island beach was large, and appeared to be greatest on those types of beach having the most nests. Whether this was due to the abundance of nests or to more favorable environment for the crabs is not known. The wide sloping beach that had the most nests (1 every 28 feet) also had the greatest amount of crab predation, 60.9 percent of the 110 nests made on that type.

Raccoon. Raccoons destroyed 5.6 percent of the total number of nests. Predation by this animal was decidedly higher in previous years, and the decline is attributed to control measures during the winter months. A wide variety of foods on wooded Bull's Island makes raccoon depredation of turtle nests there low. On Cape Island with its limited flora and fauna, raccoons must depend for their food on fiddler crabs, oysters, insects, mice, bird eggs, and turtle eggs. Twenty-four raccoon droppings collected throughout June, July, and August from Cape Island contained remains of fiddler crabs (100 percent) with a trace of insect matter (*Coleoptera*). In fact, fiddler crabs are the major year-round raccoon food on Cape Island. With such a limited diet, it is little wonder that raccoons relish loggerhead eggs.

On Cape Island raccoons patrolled the beach and dunes singly or in family groups of two or three. It is our belief that nest depredation was carried on by relatively few individuals who covered the same area throughout the summer. The behavior of these animals around nests was irregular. Many times they walked directly over egg deposits the night they were laid, not even pausing to investigate. Freshly made nests with crab burrows down to the eggs and shells scattered on the surface would also fail to arouse the curiosity of passing raccoons. Other nests were raided the night they were made or even many days after incubation had started and the site had been obliterated. The entire clutch of fresh eggs was usually eaten after they had been reached through a large excavation, and the shells scattered on the surface. Sometimes a few dozen eggs were left intact in the bottom of the nest. Eggs that contained developing young were broken and scattered rather than eaten, and especially when the embryos were almost ready to emerge. Young loggerheads are doubtlessly caught and eaten by raccoons. Around one nest that had hatched the preceding night we found six young turtles with their heads missing; tracks indicated this was raccoon work.

Erosion. Another agency of nest destruction on Cape Island was erosion by the action of the surf. The periods of greatest loss occurred whenever the highest monthly tides were accompanied by a strong wind. Nests uncovered by the pounding of the surf were immediately entered by sand crabs. As shown in Table 7, most washing (90 percent) occurred on the low beach below the truncate dunes, a type that was chosen least by nesting turtles. On the other hand, the least damage (1 percent) was on the wide sloping beach, the type most used by the female loggerheads; this stretch of beach is much higher than the former.

Invertebrate Life in the Nest

Nests opened by predators soon develop a population of flies and beetles, attracted for feeding and egg-laying. Such concentrations attract birds; turnstones and sanderlings have been observed feeding around the opened nests. Small nematodes commonly develop on broken eggs. Mites collected from the plastron sutures of a hatchling loggerhead were identified as *Macrocheles* sp. (Parasitidae) by Dr. Ewing of the U. S. National Museum, who stated that the group is not parasitic and doubted "its specific association with the turtle."

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